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# SOME ASPECTS OF THE BIOLOGY OF THE MARINE POLYCHAETOUS ANNELID OPHELIA DENTICULATA, VERRILL 1875

CLAUDE RAYMOND GILMORE

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# SOME ASPECTS OF THE BIOLOGY OF THE MARINE POLYCHAETOUS ANNELID *OPHELIA DENTICULATA* VERRILL 1875

BY

CLAUDE RAYMOND GILMORE

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Marion N. Pettibone

Albin R. Hodgdon

Burton C. Staysead

Emery F. Swan

George M. Moore

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# SECTION I

## INTRODUCTION

Verrill (1875) described the species Ophelia denticulata from one specimen that was dredged in 14 fathoms of water off Block Island, Rhode Island. His description was very brief, confined to a foot-note, and included the following data; "Body long and round; 9 anterior segments with short setae; 18 with slender, tapering branchiae, denticulate on the front edge; 5 caudal segments with long setae; anal segment with 16 to 18 slender acute papillae, and two large lanceolate ones below. Length 70 mm.; diameter 6 mm.". Verrill's illustration of O. denticulata appeared later in 1881.

Schneider (1887), upon receiving some opheliids from Pouliguen, France, found that the specimens did not fit the description of Ophelia bicornis Savigny or any other Ophelia listed for France. Therefore, not having access to a good library, he provisionally named the opheliids Ophelia neglecta. All his specimens possessed 18 pairs of branchiae, from the 10th. to the 27th. setigerous segment inclusive, and had 32 setigerous segments. The anus was surrounded by a collarette of 20 simple papillae of which the "inferior two proceed directly from the body". The branchiae were described as being cirriform and having

"small papillae" on the anterior border. Schneider also included descriptions of the parapodia, mouth, lateral and ventral grooves, and the nervous system.

Hartman (1942) referred O. denticulata to O.limacina Rathke but Pettibone (1956) pointed out that the species in question could be readily separated on the basis of morphological differences and that O. denticulata should not be referred to O. limacina.

After examining data on the type specimen of Ophelia denticulata sent to him by Dr. Fenner Chase of the Smithsonian Institution, Tebble (1953) had no doubt that Ophelia neglecta and Ophelia denticulata were conspecific. The name Ophelia denticulata Verrill, 1875, had taxonomic priority over Ophelia neglecta Schneider, 1887; therefore, the name Ophelia denticulata Verrill stands as the proper name for the species.

Hartman (1959) appears to have some reservations concerning the synonomy for she lists both O. denticulata and O. neglecta indicating that O. neglecta is "perhaps the same as O. denticulata".

Distribution. Distributional records for O. denticulata, usually listed as O. neglecta, indicate that this species is present on the coasts of France bordering the Atlantic, the Mediterranean, and the English Channel.

Fauvel (1907, 1925, 1927) lists Youdet and Terrenes and "perhaps Roscoff" on the coast of the English Channel; Pouliguen,Lorient, and Noirmoutier on the Atlantic Coast

as being areas from which O. neglecta has been collected in France.

Tebble (1953) states that O. denticulata is "well known from the Mediterranean and Atlantic coasts of France".

The only published records of the occurrence of O. denticulata in North America are:Verrill's (1875) record of a specimen dredged off Block Island, Rhode Island in 14 fathoms; Sumner, Osburn, and Cole's (1913) record of one specimen dredged in 5 fathoms in Vineyard sound (Fish Hawk station # 7540) ; and the recent find by Wells and Gray (1964, p. 74) from Cape Hatteras, North Carolina.

The population which served as the source of material for this study was located in the intertidal sand flats of Hampton Harbor, New Hampshire by Dr. M.H. Pettibone.

Papers published by Schneider (1887) and de Saint-Joseph (1898) are the only ones having detailed descriptions of the morphology and anatomy of O. denticulata (as O. neglecta). Both Schneider and de Saint-Joseph give fairly detailed descriptions of the external morphology.

In regard to the internal anatomy, Schneider concerns himself mainly with a description of the nervous system, comparing it with that described for O. bicornis by Pruvot (1885) and with the description by Kukenthal (1887) of the nervous system of O. radiata. De Saint-Joseph (1898) described in some detail the divisions of the alimentary canal, the "injector organ", muscle layers, nephridia and particularly the "rod cells" of the coelomic fluid.

Unfortunately, even though many of the structures described by de Saint-Joseph are done accurately, there are a few contradictory statements and salient inaccuracies which detract from the value of the paper.

Other publications on O. denticulata are scarce. Hartmann-Schröder (1956), in a study of the comparative anatomy of Opheliidae, apparently had no specimens of O. denticulata and refers to the work of de Saint-Joseph (1898) when discussing O. denticulata. Brown (1938), in a publication on O. rathkei (as O. cluthensis) McIntosh, also refers to de Saint-Joseph (1898) when comparing O. denticulata with O. rathkei.

Other publications are either concerned with the taxonomic description of O. denticulata per se (Fauvel, 1907, 1925, 1927; Tebble, 1953) or its synonymy (de Saint-Joseph 1898; McIntosh, 1908; Benham, 1916; Monro, 1936; Hartman, 1942 ; Pettibone, 1956).

In view of the fact that the publication by de Saint-Joseph (1898) is the most comprehensive study that is now available on O. denticulata, this study is an attempt to update, correct, and supplement the work of de Saint-Joseph in this species of opheliid.

# SECTION II

## EXTERNAL MORPHOLOGY

General. The marine polychaetous annelid Ophelia denticulata Verrill is a sluggish, grub-like worm which lives in clean, coarse, shifting sand in both the intertidal and shallow subtidal regions of the marine environment.

In general outline, the body is somewhat fusiform. It tapers evenly to a point anteriorly but appears rather abruptly truncated at the posterior end. The truncated appearance is caused by a telescoping together of the last four setigerous segments. The anus is surrounded by a circlet of small lanceolate papillae on the dorsal and lateral sides. There are also two larger lanceolate ventrolateral anal papillae. The ventrolateral papillae are approximately 2-3 times wider and $1\frac{1}{2}$ times longer than the dorsolateral anal papillae.

The prostomium is a small sharply pointed cone, the apex pointed anteriorly, lacking antennae, tentacles, or palps.

The ventrolateral longitudinal ridges or soles extend the length of the posterior two-thirds of the body. These ridges are bordered by a single, narrow, deep ventral furrow and a pair of wider and shallower lateral grooves, one on each side of the body.

The indonspicuous biramous parapodia and the bright

red cirriform branchiae are located on the upper side of the ventrolateral, longitudinal ridges at the bases of the lateral grooves.

The dorsal surface above the lateral grooves is uniformly rounded in the posterior region. The anterior third of the body, which lacks the ventral and lateral grooves described above, is somewhat flattened ventrally and convex dorsally.

Larger living specimens (40-100mm.), which lack sex products, are a purple gray color with an iridescent sheen. Striations on the cuticular surface cause this iridescence. Sexually mature individuals, whose coelom is packed with either yellow eggs or creamy white sperm, exhibit either a light buff or a pinkish-white color and also have an iridescent sheen. Smaller specimens (25-30mm.), which have a comparatively thin cuticle through which the blood in the large sinuses can be seen, are a light red color. Preserved specimens are uniformly light or dark gray color with brown branchiae.

Males and females can usually be differentiated on the basis of body color but this system is not infallible. Females are usually distinguished by their patchy buff color whereas mature males are usually a uniform creamy-pink color. As the female becomes increasingly packed with eggs, the patchiness disappears and the whole body becomes lighter in color. At this stage it is very easy to mistake a female for

a male. A more reliable method is to observe the everted proboscis of the specimen in question under a dissecting microscope. If it is a female, the eggs are readily visible through the thin wall of the proboscis. Sperm, of course, are invisible but, if the specimen is obviously mature and eggs are not visible in the everted proboscis then it is probably a male. It is not possible to distinguish the sex of immature worms.

The genus Ophelia is usually characterized as having two body regions (Fauvel, 1927): a swollen, cylindrical anterior region (thoracic region), and a posterior region with a deep ventral groove and two lateral grooves (abdominal region). The last few setigerous segments differ markedly from the more anterior segments such that it should be considered as a separate morphological third body region (caudal region). Tebble (1952) characterized the species of Ophelia as having three body regions: an anterior abranchiate region, a branchial region, and a posterior abranchiate region. Tebble (1952) relies heavily on this posterior abranchiate region in his argument to validate O. borealis, O. limacina, O. roscoffensis, O. bicornis, and O. rathkei as separate species. The thoracic, abdominal, and caudal regions correspond to the prebranchial, branchial, and postbranchial regions in O. denticulata. I shall therefore characterize O. denticulata as having three body regions: prebranchial region, branchial region, and postbranchial region.

Prebranchial region of Ophelia denticulata. The prebranchial region is composed of the prostomium, peristomium, and nine setigerous segments. The length of this region is approximately one-third the total body length and the width, at the widest point, is approximately one-tenth of the body length.

It is difficult to determine the limits of the prostomium and peristomium, since there is no externally visible dividing line and there are no appendages associated with the peristomium. The parapodia of the first setigerous segment are directly above the mouth. Thus, it is evident that at least one trunk segment has fused with the mouth region during the formation of the peristomium.

The palpode, the anterior-most extremity (fig. 1) is a smooth cone which is capable of movement independent from the rest of the body. The base of the palpode is continuous with the annulated region and is separated from it by a very shallow groove. The dorsal part of the base of the palpode extends slightly more posteriorly than the ventral part. A single pair of lens-shaped nuchal organs is located laterally and slightly dorsally immediately posterior to the junction of the palpode and the annulated region. When invaginated, the nuchal organs appear as small dorsolateral slits with a small protuberance on the anterior border. When everted, the nuchal organs appear hemispherical.

The annuli, which are ridges of the cuticle thickened

on the posterior edge, overlap posteriorly giving a shingle-like appearance. There are usually from 23-25 prominent annuli from the base of the palpode to the first pair of parapodia. A pair of dorsolateral depressions, representing the attachment of the labial muscles, appear in the region of annulus 21 (fig.2 ). Numerous minute pores pierce the cuticle in the region between the annular ridges. The annuli do not form complete rings and may also branch at least once. The pores immediately anterior to the parapodia are larger than in other regions. There are 5-6 annuli per segment in the prebranchial region.

The ventral mouth, a transverse slit with an anterior and a posterior lip, is in line with and ventral to the first pair of parapodia. A pair of prelabial grooves, caused by the attachment of the oblique muscles, run posteriorly from the base of the palpode, where they almost meet, to the lateral corners of the anterior lip. The area between the grooves is somewhat raised and the annuli in this region are more wavy appearing. The anterior lip is smooth, bulbous, and comes to a point at each corner. The posterior lip appears somewhat triangular with its apex truncated. It is also smooth with annulations appearing only at its posterior extremity.

A pair of shallow ventral grooves (postlabial grooves) extend on each side of the ventral midline from the base of the posterior lip to the posterior margin of the

ninth setigerous segment. The area between the grooves is also slightly raised but the annuli are continuous with those dorsolaterally. A pair of dorsolateral grooves extends from beneath the nuchal organs to the pit of annulus 21 and continues posteriorly above the parapodia as far as setiger 11. Depending on the state of preservation of the specimens, (i.e. how well relaxed), these grooves may appear shallow or deep. The dorsolateral pair of grooves represents the dorsal attachment of the oblique muscles and the ventral pair of grooves represents the ventral attachments of the oblique muscles.

The unarmed proboscis, a thin walled, button-shaped, lobed organ, appears blood-red when everted. Although the proboscis is typically button-shaped, it does not assume a terminal position when fully everted as does the proboscis of O. bicornis. The prebuccal region of O. denticulata may be turned upward when the proboscis is fully everted but the proboscis remains ventral.

The anterior region contains nine setigerous segments each of which bears a pair of biramous parapodia. The parapodia are typically inconspicuous being reduced to not much more than two bundles of fine, capillary setae. The parapodia in each segment are superficially quite similiar. Each ramus of the parapodium bears a small presetal and postsetal lobe (fig.2 ). The presetal lobes of both the noto- and neuropodia are fleshy, ellipsoid protuberances lacking additional processes. The notopodial

postsetal lobes are crescentric and do not protude as much as do the presetal lobes. The dorsal parts of the neuropodial postsetal lobes contain small dark depressions covered by lip-like folds with a small pit at its tip. The lateral organs are small protuberances covered by a very thin hemispherical section of cuticle. They are located between the noto- and neuropodia of each of the 32 segments. Both the notopodium and the neuropodium bear two groups of setae, an anterior group and a posterior group which are subequal in length. The posterior group of setae are approximately two times longer than the anterior group in the anterior parapodia. In the succeeding segments, the posterior group of setae becomes progressively longer. The anterior group of setae remains short. The anterior group of noto-and neurosetae curve toward each other so that they just meet over the lateral organ (fig. 2 ).

All the parapodia of the prebranchial region are essentially as described above with the exception of those of the first and ninth setigerous segments. In the first setigerous segment, the parapodia are greatly reduced and easily overlooked. The presetal and postsetal lobes are minute elevations and only rarely is the small pit of the postsetal neuropodial lobe present. In the ninth setigerous segment large glandular swellings are present dorsal to the parapodia, extending dorsally to the point of attachment of the oblique muscles and ventrally to the level of the noto-

podium. The lobe is low in the anterior part of the segment and reaches its maximum height at the posterior border of the segment. The notopodial presetal lobes are reduced and tilted anteriorly by this protuberance.

In cross section, the anterior region would be circular if it were not for the oblique muscles. The bilaterally paired oblique muscles attach dorsolaterally and angle toward the midventral line attaching on either side of the ventral nerve cord. Upon contraction, these muscles depress the dorsal body wall on either side of the dorsal midline and slightly elevate the ventral body wall on either side of the ventral nerve cord. The result is that the anterior region becomes subtriangular (fig. 15 ).

Discussion of the Prebranchial Region. Anderson (1959) states that the polychaete prostomium and mouth region are probably presegmental structures. However, in the formation of the peristomium, one or more trunk segments may fuse with the mouth region. The relationship of the prostomium, peristomium, and the first two trunk segments in the Opheliidae is somewhat confused. In Ophelia bicornis Savigny, Wilson (1948) has shown that the prostomium fuses with the peristomium leaving a conspicuous groove between them in the 19th day larvae. There is also a well marked groove between the peristomium and the first trunk segment. Since Wilson was unable to rear any further stages

he could not say whether or not there was any additional fusion of segments. Adults of Ophelia bicornis, as in O. denticulata, do not have any conspicuous grooves between the prostomium and the peristomium or between the peristomium and the first trunk segment. If there is no loss of parapodia and setae from the first trunk segment, then its being in line with the mouth would indicate that the prostomium, peristomium, and first trunk segment are fused. Because of the great similarity among the species in the genus Ophelia, it seems reasonable to assume that the same is true for O. denticulata.

In describing the development of Euzonus (Thoracophelia) mucronata (Treadwell), Dales (1952) indicates that the region between the mouth and the first setigerous segment, though achaetous, represents the first true segment and not the peristomium, as suggested by Wilson (1948). Dales further suggests that the first setigerous segment in both O. bicornis and E. mucronata represents the second trunk segment. According to Dales, then, the position of the first setigerous segment in the adult Ophelia would indicate that at least two trunk segments are fused to the mouth region in the formation of the peristomium.

The larvae of Armandia brevis (Moore), reared by Hermans (1964), are very similiar to those of E. (Th.) mucronata in the early stages. In the larvae of A. brevis, Hermans (1964) noted a structure between the mouth and the

first setigerous segment which was very similiar to that termed the first trunk segment by Dales (1952). Hermans (1964)called this structure a lower lip and noted that it appeared to invaginate to form part of the proboscis. If the structure that Dales (1952) identified as the first true segment in E. (Th.) mucronata and the structure identified by Hermans (1964) as the lower lip in A. brevis are the same, then it would appear that the prostomium, mouth region, and first trunk segment are fused in those opheliids in which the larval development has been studied.

The conical palpode is evidently only part of the prostomium. Hartmann-Schröder (1956) has described the development of the larvae of Ophelia rathkei McIntosh from the thirteen segment stage up to the twenty-four segment stage. These are the stages in which the prostomium takes on the form of that of the adult. In the 13 to 18 segment stages, the prostomium is still rounded and becomes less well separated from the first segment. In the latter part of the 18 segment stage, the prostomium becomes conical and there is no visible separation between it and the first segment. Also, two nerves have grown anteriorly from the brain. By the 22 segment stage, the palpode (Stirnpapille), containing the two large nerves, is formed on the anterior border of the prostomium. Dales (1952), though not able to raise metamorphosing larvae beyond the stage at which they

were ready to settle, indicates that the prostomium of E. mucronata does not become pointed until the worm is about two mm. long, approximately the same length as in O. rathkei. The palpode of Armandia brevis grows out from the anterior edge of the prostomium in much the same way as described for O. rathkei (Hermans, 1964).

The larval development of the different species of the Opheliidae that have been studied to date is so similiar that one would not expect the larval development of O. denticulata to differ drastically.

Branchial Region. The branchial region is composed of 18 setigerous segments including almost all of the posterior two-thirds of the body length. As in the anterior region, each segment bears a pair of biramous parapodia. The body is rounded dorsally. There is a deep midventral groove and a pair of lateral grooves. The lateral grooves of the branchial region are not continuous with the dorsolateral grooves described for the anterior region although they both result from the dorsal attachments of the oblique muscles. The lateral grooves begin at the junction of setigerous segments 9 and 10, the lower margin of the groove being in line with the upper part of the neuropodial presetal lobe. The lateral grooves extend about a third of the way up the lateral body wall.

A series of vertical rows of minute pores, termed branchial fenestrations by Tebble (1953), extend from the

level of the lateral organs to the midlateral parts of the body wall in all of the branchial segments except the first. The rows are usually incomplete, some starting higher up than others and some ending before they reach the upper limits reached by others. The rows of pores are usually straight but, in some individuals, they may be very sinuous in some of the segments (fig.5).

The midventral groove, between the ventrolateral ridges, begins at the junction of setigerous segments 9 and 10 and continues the length of the branchial region. The last annulus to extend completely across the ventral surface marks the end of setiger 9. Immediately posterior to this annulus, the ventral annuli are separated by a region containing rows of pores. The ventral groove is lined with these pores. On each of the ventrolateral ridges, at about the level where the longitudinal muscles end and where the attachments for the oblique muscles begin, the cuticular annuli leave off and rows of pores or branchial fenestrations begin. Even if the oblique muscles are totally relaxed, or even stretched, so that the ventral lateral grooves are not evident, the junction of setiger 9 and 10 are still discernable by the pores characteristic of the ventral groove. The posterior border of the large lateral glandular ridges also marks the posterior border of setiger 9. (fig. 1).

The annuli form a semicircle over the dorsal surface, ending above the rows of branchial fenestrations. The dorsal annuli are distinct up to branchial segment 11 or 12 although becoming fewer in number. The first branchial segment has six annuli. Branchial segment 12 has four annuli. The dorsal annuli disappear at about branchial segment 13. The next annulus appears on the posterior end of the branchial segment 18. Ventrolateral annulations begin again on a level with the neuropodial presetal lobe continuing on the ventrolateral ridge to the beginning of the midventral groove. Many annuli are incomplete. The annuli of the ventrolateral ridge are present up to branchial segment 13. In the region where the annuli are present on the ventrolateral ridge, there is a very conspicuous ridge of cuticle that begins at the base of the neuropodial presetal lobe and continues part way into the midventral groove.

The parapodia are located at the junction of the lateral groove and the ventrolateral ridge at the posterior margin of the segment. They are similiar to the parapodia of the prebranchial region in that they are biramous, reduced, and include a lateral organ between the two rami; each ramus bears two groups of capillary setae. The neuropodia are composed of small, fleshy presetal lobes and minute postsetal lobes. The postsetal lobes, as in the anterior region, have small areas in which the cuticle is

thin giving the lobe a bilobed appearance. The neuropodial setae are in two groups; an anterior and a posterior group subequal in length. A deep groove marks the posterior border of each of the branchial segments. The segments increase in length from anterior to posterior, the posterior segments being about twice as long as the anterior segments.

The branchiae, which are outgrowths of the notopodia, dominate the notopodial region. All that remains of the notopodial region is a small presetal ridge, a setal slit, and notosetae which fan out at the base of the branchia. The base of the branchia is a slight vertical elevation of the body wall which extends into the lateral groove.

There are 18 pairs of simple, cirriform branchiae in setigerous segments 10-28. They are either smooth or have accordion-like folds depending upon their state of contraction. The anterior margin of the branchiae is denticulate along most of its length in all but the last five or six pairs of branchiae. The branchiae decrease in length from anterior to posterior, the anterior-most pairs being as much as five or six times longer than the last pair. The first pair, when laid back along the body, may extend as far back as branchial segment 7. The branchiae are contractile, capable of increasing or decreasing in length, and, in living specimens, may be coiled or curved anteriorly. The surface of the branchiae is ciliated. The action of the cilia results in a general movement of water along the body from anterior to posterior.

In some specimens it has been noted that parts of the branchiae which have been damaged or lost have been regenerated.

The branchiae are usually very constant in number and form. Three specimens have been collected in which the branchiae differ from those usually associated with O. denticulata. One has a small, unpaired branchia on the left side of the setigerous segment 29. On another individual the branchia on the left side of the seventh branchial segment has a small branchial outgrowth in the middle of the main branchial filament. In the third, and most interesting, individual, compound branchiae were found on the anterior branchial segments. On the right side of the body, branchial segments 2,3,4,5,7,8, and 9 contain branchiae with three filaments. The largest filament is lateral and appears the same as a normal branchial filament. The two medial filaments are shorter and may be separate or have a common base. The main branchial filament of the seventh branchial segment has a short additional outgrowth about one-third of the distance from the base to the tip. The left side of the body has compound branchiae on the branchial segments 1,2,3,4, and 5. Branchial segments 1, 3, and 4 contain compound branchiae with three filaments but the two smaller filaments of the first branchial segment and the large main filament is medial. The compound branchiae of the second and fifth branchial segments contain two

filaments, the smaller filaments being medial in both segments. The smaller filament of the second branchial segment occurs part way up the main filament; that of the fifth branchial segment occurs at the base of the main filament.

Other than the deviation in the form of the branchiae, the specimen agrees with other specimens of Ophelia denticulata.

The noto- and neuropodial setal groups are similiar to those described for the anterior abranchiate region. Each ramus of the parapodium bears two groups of capillary setae. The anterior curved group of notosetae is about as long as those of the neuropodium. The posterior group of notosetae is about twice as long as those of the neuropodium, whereas, in the anterior abranchiate region, the noto- and neuropodial posterior groups of setae are of equal length.

Additional structures are found in the branchial region. Six pairs of nephridia, which open to the outside through nephridiopores, are located on the third through the eighth branchial segments inclusive. The nephridiopores are located on the middle of the segment about half way between the parapodia of the two adjacent segments and in line with the lateral organs. The nephridiopores have a raised margin of thickened cuticle. They are oval in shape, the vertical axis being longer. In an individual of 100mm. in length, the nephridiopores, which are all approximately the same diameter, have a diameter of 0.02mm. There are no external folds or lips guarding the nephridiopores. A

fold of the distal, posterior portion of the nephridial tubule, which is visible from the outside, may serve to block the entry of foreign particles. In preserved specimens, although the nephridiopore itself appears to be open, the fold of the tubule practically occludes the passageway so that only a small vertical slit remains (fig. 5).

Occasionally a specimen is seen with more than six pairs of nephridiopores. Additional nephridiopores may occur either on the second branchial or ninth branchial segment and may or may not be paired. The openings of these additional nephridiopores are usually smaller in diameter.

Minute lateral pores, usually two pairs of vertically arranged openings per segment, are found in the eleven segments posterior to those bearing the large nephridiopores. The pores are located on the ventrolateral ridge in the posterior third of the segment with the upper member of the pair being in line with the neuropodial presetal lobe. The ventral member of the pair is located slightly below the lower edge of the neuropodial presetal lobe. Posteriorly, the pores become progressively lower on the ventrolateral ridge so that, in the last few branchial segments and in the first postbranchial segment, the upper pore is located below the lower edge of the neuropodial presetal lobe. The pores are minute and easily overlooked the largest being between 0.03 and 0.06 mm. in diameter. In addition, a specimen that has been preserved in a coiled position often has many folds and creases in the body wall which may hide

the pores. It is extremely difficult to locate the lateral pores in specimens smaller than 60 mm. The size of the lateral pores is extremely variable, sometimes being as large as the nephridiopores. If any of the pairs of pores are lacking, it is usually those of the ninth branchial segment. Occasionally a third pore is visible in one or more of the segments and often one member of a pair of pores is missing. Variability in the total number of pores is probably not as great as it appears at first because of the difficulty in determining the presence or absence of the pores.

Postbranchial Region. The postbranchial region of Ophelia denticulata is composed of five setigerous segments and the pygidium. The postbranchial segments become progressively shorter from anterior to posterior. A deep groove between setigerous segments 27 and 28 marks the border between the branchial region and the postbranchial region. Segmentation in this region is made more evident by the deep grooves between each of the segments. The intersegmental grooves are so deep that the ventrolateral ridge is given a moniliform appearance (figs. 6 and 8).

In well contracted individuals the first postbranchial segment has the appearance of a hood under which the dorsal part of the following four segments are sheltered. When viewed dorsally, the posterior border of the first postbranchial segment is in line with the anterior border of the pygidium. In more relaxed individuals, the grooves between the segments

are still evident but not as deep. The last four segments are not folded under the first postbranchial segment but the height of the segments decreases rapidly from anterior to posterior. The distance between the first postbranchial segment and the pygidium is short because the dorsal parts of the last two setigers are tipped anteriorly (fig. 6).

The ventral groove is continuous with that of the branchial region. It widens slightly in the region of the first two postbranchial segments, then it narrows rapidly becoming a slit between the two ventral anal papillae. The rows of pores, which are found lining the grooves in all the segments of the branchial region, are found only in the ventral groove of the first postbranchial segment.

The ventrolateral ridge is higher in the first two postbranchial segments, tapering rapidly in the last three segments and ending in the lanceolate ventral papillae of the pygidium. The parapodia are in the same position relative to the lateral groove and ventrolateral ridge as those in the branchial region. They appear to be higher up on the lateral body wall because of the increased height of the ventrolateral ridge. The posterior dorsal margin of the ventrolateral ridge of each postbranchial segment is elevated into a peak almost obliterating the lateral groove. The notopodia are located at the apex of the peak. Although barely visible in the last two setigerous segments, the lateral organs are present between the parapodial rami.

Notopodial and neuropodial presetal lobes are very prominent on the first three postbranchial segments but reduced to slits in the last segments. Postsetal neuropodial lobes, branchial fenestrations, and lateral pores are present on the first postbranchial segment only. Pores through the cuticle of the dorsal body wall are evident in the first postbranchial segment only. Both anterior and posterior groups of setae are present in the noto- and neuropodia of the first postbranchial segment. The anterior groups of notosetae are short and only slightly curved ventrally. The posterior groups of setae are at least twice as long as that of the preceding segment (last branchial segment). The neurosetae are also in two groups. The anterior groups are almost as long as the posterior groups and curve dorsally toward the lateral organs. The posterior groups are only one-fifth as long as that of the notopodia but the setal groups do not curve ventrally as in preceding segments. The anterior groups of setae may not be distinct groups but just small replacement setae of the posterior group in these segments.

The neurosetae of the second postbranchial segment are about one-third as long as the notosetae. In the third postbranchial segment the neurosetae are about one-half as long as the notosetae. The fourth and fifth postbranchial segments contain only one group of long, capillary setae in both the noto- and neuropodia. The neurosetae are equal in length to the notosetae. The setae in the last four post-

branchial segments project back as far as the pygidium but only those of the last two segments project beyond the pygidium. Of all the 32 setigerous segments, the longest setae occur on segment 30 (third postbranchial segment).

It would appear, at first, that the first postbranchial segment, having so many structures in common with the branchial region, should morphologically be considered to be more allied with the branchial region than with the postbranchial region. The fact that one individual has been observed to have developed a small gill on this segment tends to reinforce this argument. But, since almost all O. denticulata lack branchiae on this segment, and it is always clearly defined from the preceding segments, I feel that this segment should be included with the rest of the postbranchial segments.

Pygidium. A shallow groove separates that last postbranchial segment from the pygidium. The pygidium is an achaetous segment bearing the anus and a circlet of lanceolate anal papillae and two larger lanceolate ventral papillae. The anal papillae extend upward and backward around the anus. These papillae never contract tightly around the anus as they do in O. rathkei or O. limacina.

The circlet of anal papillae usually numbers 17-18 but there may be as few as 13 or as many as 22 papillae in some individuals. The bases of the papillae are fused in the dorsal part of the pygidium and the tips may be entire or split distally. The middorsal papillae may or may not

be shorter than the dorsolateral papillae.

In lateral view, the dorsal part of the pygidial segment, where the bases of the anal papillae are fused, is longer than the ventral part. This portion of the pygidium is wedge-shaped, with the apex of the wedge pointed ventrally. The two ventral papillae are continuous with the ventrolateral ridge of the preceding region. The medial bases of the two ventral papillae curve dorsally and fuse forming the base of the anal valve. The anal valve extends dorsally to the dorsal part of the anus then curves laterally to the left side and continues into the posterior part of the intestine (rectum). Externally, 10-13 digitiform papillae are visible on the posterior border of the anal valve. Ciliated organs are located in folds of the anal valve. The ciliated organs extend the length of the rectum.

# SECTION III

## TAXONOMIC CONSIDERATIONS OF THE FAMILY OPHELIIDAE

Introduction. The division of the Class Polychaeta into two subclasses, that of Errantia and Sedentaria as used by Fauvel (1923) and others, is not a natural division nor are there sharp morphological distinctions between them. However, if one is aware of the general characteristics of each subclass, these taxa can be useful as a general means of categorizing polychaetes. Thus one can generally categorize an individual polychaete or a group of polychaetes, on the basis of morphological characters, as an errant type, a sedentary type, or as a type having characteristics intermediate between the two.

According to Fauvel (1923), the body or metastomium of members of the errant group is composed of a repetitive series of similiar segments and is not divided into regions. The cephalic lobe or prostomium bears palps, antennae, and eyes. The peristomium usually bears tentacular cirri. A muscular proboscis bearing chitinous jaws is present. The parapodia are typically biramous, both rami originating from a common base. The notopodial and neuropodial rami are each supported by an aciculum. Appendages, such as parapodial lobes (ligules), dorsal and ventral cirri, are usually present. Reduction of the notopodial lobe is common, resulting in subbiramous, sesquiramous, or uniramous parapodia. Branchiae, when present,

are associated with the parapodia and are found on most of the body segments. Internally, septa are located between each segment and nephridia, of various types, are found in each segment.

In the sedentary polychaetes, the body is usually divided into two regions, a thorax and an abdomen. The head does not bear palps or antennae but may bear a branchial plume. A proboscis, if present, is usually thin walled, saclike, without jaws. The two rami of the parapodia are distinct and more or less separated from each other. The neuropodial ramus is often reduced to an uncinigerous torus with short setal hooks. The abdominal region may lack notopodia (Terebellidae). Branchiae are frequently located in the anterior region only and are few in number. Septa are less numerous than in the errant group. The thoracic region, with the exception of the first few segments, usually lacks septa. The nephridia are reduced in number and are usually found in the thoracic segments. In some, the anterior nephridia serve as excretory organs and the posterior nephridia serve as gonoducts.

As pointed out by Quatrefages (1865) and Støp-Bowitz (1945), the family Opheliidae is morphologically intermediate between the errant and sedentary types. The body may or may not be divided into regions. The head (prostomium and peristomium) is reduced to a conical or rounded structure which bears neither palps, antennae, nor tentacular cirri. The proboscis is thin walled, saclike and unarmed. The peri-

stomial segment is setigerous. Eyes are embedded in the brain and, in some genera, additional eyes are located laterally in some of the body segments. The parapodia are reduced to small bundles of capillary setae. Small, fleshy presetal lobes may be present or absent. Neither supporting acicula nor uncini are present in the parapodia. Branchiae may be present or absent; when present, they may be located on most of the body. They may be cirriform, bipinnate, pectinate or dendritic. Internally, septa are confined to a few segments posterior to the peristomium and to the last few setigerous segments. In some genera, the anterior septa become modified into a muscular, conical sac (injector organ). Nephridia are usually numerous and, except for Euzonus, they are open to the coelom. Two types of nephridia are found in some species of Ophelia.

The degree of development of the ventral groove in the Opheliidae is related to the number and thickness of the oblique muscle bands. Both McIntosh (1915) and Tampi (1959) have pointed out that there is an increase in the development of the oblique muscles from Travisia (no ventral groove) to Polyopthalmus and Ammotrypane (ventral groove extends length of body). The genera can be divided into four groups based on the extent of the ventral groove (table III).

The genera of Group I (Ammotrypane group, table III) have a ventral groove which extends the entire length of the body. The genera Antiobactrum Chamberlin and Ammotrypanella

McIntosh are each represented by a single, poorly known species. According to McIntosh (1879), Ammotrypanella has filamentous or cirriform branchiae located only in the posterior region. The setae of the first 7-8 setigers are longer than those of the following segments. There are no lateral eyes. A pair of small, dark pigment spots is located at the base of the prostomium. The pygidial segment is formed into a long anal tube. Ophelina brasiliensis Hansen, being preoccupied, was renamed Antiobactrum by Chamberlin (1919). Hansen described the type specimen as having 34-36 cirriform branchiae. In addition, the long anal tube, which has a short, median anal cirrus, is open or split ventrally. Ammotrypane Rathke, Armandia Filippi, and Polyopthalmus Quatrefages have an elongate, narrow body, not divided into regions and are superficially similar to Amphioxus (Fauvel, 1927). The three genera have an elongate anal tube which bears small papillae and a long, deciduous, median anal cirrus is present in Ammotrypane and Armandia. Simple, cirriform branchiae occur on most of the setigerous segments in Ammotrypane and Armandia, but are lacking in Polyopthalmus. A row of lateral eyes occurs on each side of the body in Polyopthalmus and Armandia. The prostomium is conical in Ammotrypane and Armandia but is trilobed in Polyopthalmus when the large nuchal organs are everted.

Group II is confined to the genus Trachytrypane McIntosh. The body is very elongate and shaped superficially like Ascaris (Fauvel, 1927). The ventral groove is confined to

the posterior half of the body. Branchiae, lateral eyes, and anal papillae are absent. The pygidium has a short anal tube and the prostomium is conical.

Group IV includes Travisia Johnston and Kesun Chamberlin. The body, which is rounded anteriorly and slender and rectangular posteriorly, is short, grub-like and lacks a ventral groove. The parapodia may be reduced to just bundles of setae without parapodial lobes or conspicuous parapodial lappets may be present (Travisia). Cirriform branchiae are present on most of the setigerous segments in Travisia, and are lacking in Kesun. Also, the pygidium is cylindrical and longitudinally furrowed in Kesun and is button-like with fused papillae in Travisia.

Group III includes Ophelia Savigny, Euzonus Grube, and Euzonus (Thoracophelia) Ehlers. In these genera, a deep ventral groove and a pair of ventrolateral ridges are located on the posterior two-thirds of the body. Anteriorly, the body is somewhat swollen and rounded. Glandular ridges may occur in the anterior (thoracic) region. The branchiae are located in the posterior two-thirds of the body. In Euzonus, a deep constriction occurs at the posterior margin of setiger two and the setae of this segment are longer than those of the other thoracic setigers. The posterior-most setigers are telescoped together and the pygidial segment is terminated by a single ventral anal papillae, surrounded by a circlet of smaller anal papillae. The branchiae of the subgenus E. (Thoracophelia) are twin filaments and those of

the subgenus E. (Euzonus) are dendritic or pectinately branched. The branchiae of the genus Ophelia are usually simple cirriform filaments. However, the branchiae of O. ashworthi are twin filaments and O. anomala lacks branchiae. In none of the species of Ophelia is the second setigerous segment enlarged.

## SECTION IV

## TAXONOMIC CONSIDERATIONS OF THE GENUS *OPHELIA*

Fauvel (1927) utilized the number of pairs of branchiae and the presence or absence of dorsal longitudinal ridges on the posterior part of the body to identify the four species of *Ophelia* present on the coasts of France.

Tebble (1953) constructed a key in which two species were separated from the rest on the basis of the form of the branchial filament (i.e., single or twin filaments) and the number of ventral anal papillae (one or two). The remaining species, all of which have single branchial filaments and two ventral anal papillae, were separated on the basis of the disposition of setigerous segments. Tebble (1952, 1953) devised a method whereby the disposition of setigerous segments of species of *Ophelia* can be indicated by means of a body formula based on the number of branchial segments (b) and their positional relationship to the abranchiate segments (a). For example, the body formula of *O.denticulata* is : 9a + 18b(3b-8b) + 5a=32. That is, there are 18 branchial segments (18b) bearing six pairs of nephridiopores located on branchial segments three to eight (3b-8b). There are nine abranchiate (9a) setigers located anterior to the branchial region and 5 abranchiate setigers (5a) located posterior to the branchial region. There is a total of 32 setigerous segments. Tebble pointed out that the following morphological characters also serve as diagnostic characters of varying importance : the presence or absence of a series of irregular vertical rows of minute pores in the lateral

grooves (branchial fenestrations), the structure of the posterior region, chaetous or achaetous anal segment, extent of the ventral and lateral grooves, and shape of branchiae. Although not mentioned by Tebble, the presence or absence of a pair of glandular ridges located in the posterior part of the prebranchial region and the shape of the anal papillae can be valuable in the determination of a species.

All of these morphological characters are subject to variation. The total number of setigers and the number of branchiae are dependent upon the age of the individual. Occasional abnormalities in the form of the branchiae occur. Apparent variations may arise due to the accidental loss of branchiae or setae. The effects of various preservatives may alter the appearance of the specimen. For example, if the specimen is improperly preserved, abnormal swelling may obscure the extent of the ventral and lateral grooves.

The number and location of the branchiae has been found to be quite variable in some species of Ophelia e.g., O. rathkei, O. limacina, and O. bicornis . Since the body formula is based on the number and location of the branchial segments, I feel that less variable morphological characters should be used in the determination of relationships.

One of the characteristics of the genus Ophelia, given by Fauvel (1927) and others, is that the body is divided into two morphological regions, a rounded thoracic region and an abdominal region which bears a deep ventral groove and two lateral grooves along its entire length.

The point of origin of the ventral groove is the line of demarcation between the two morphological regions. The ventral groove does not begin on the same segment in all species. I prefer to characterize the genus Ophelia as one in which the body is divided into three regions: thoracic, abdominal, and caudal. The caudal region includes those terminal setigerous segments which become modified to give the posterior part of the body either a truncated or tapered appearance.

If the shape of the caudal region and the point of origin of the ventral groove are chosen as indicators of morphological similarity, then the species of Ophelia fall naturally into two groups. One group, referred to as the bicornis group, includes those species in which the posterior setigers are telescoped together giving the posterior end a truncated appearance and in which the ventral groove begins at the anterior end of setiger 9, 10, or 11. The second group, referred to as the limacina group, includes those species in which the ventral groove begins at the anterior end of setiger 7 or 8 and which have a tapered or sloped posterior end. A third group (anomala group) can be formed from those members of the limacina group which lack branchiae (O. anomala Day), have twin branchial filaments (O. ashworthi Fauvel), or have a single ventral anal papilla (O. rathkei McIntosh and O. remanei Augener?). The remaining species in the limacina-group, as well as those in the bicornis-group, have simple cirriform branchiae and two ventral anal papillae.

The bicornis-group includes O. bicornis Savigny, O. denticulata Verrill, O. radiata (Delle Chiaje), and possibly O. bipartita Monro, and O. dannevigi Benham. The limacina-group includes O. limacina (Rathke) (including O. borealis Quatrefages and O. assimilis Tebble), Ophelia roscoffensis Augener, O. africana Tebble, O. agulhana Day, O. capensis Kirkegaard, O. formosa (Kinberg), O. magna (Treadwell), O. pulchella Tebble, and possibly O. praetiosa (Kinberg) and O. modesta Støp-Bowitz (see tables I and II).

Since the major concern of this investigation is to determine those species most closely allied to O. denticulata, only the bicornis-group will be discussed in detail. Although a comparison of the body formulae does not indicate a close morphological relationship between O. denticulata and O. bicornis, the two species share the following morphological characters: ventral groove begins at the anterior end of setiger 10 (junction of setiger 9 and 10); a pair of glandular ridges located above the notopodia of setiger 9; six pairs of nephridiopores located on setigers 12-17; truncated posterior end; anal papillae lanceolate. One of the most obvious differences between the two species, although not a valuable taxonomic character, is size. Ophelia bicornis seldom attains a length of 30 mm. compared with a length of 100 mm. for O. denticulata. The two species differ in the number, shape and location of the branchiae. In Table I the Ophelia species of the bicornis-group are compared. However, it should be pointed out that in O. denticulata the first pair of branchiae is located on

setiger 10, the first abdominal segment. The first pair of branchiae in O. bicornis, although variable in location, is never located on the first abdominal segment (setiger 10).

O. denticulata and O. radiata are similar in that they both have glandular ridges, truncated posterior end, and the first pair of branchiae begins on the first abdominal segment. The differences between the two species concern the number of pairs of nephridiopores, the location of glandular ridges, branchial fenestrations and location of the origin of the ventral groove (see Table I).

A lack of data complicates the determination of the morphological relationships between O. denticulata, O. bipartita, and O. dannevigi. Monro (1936) did not describe the shape of the posterior region of O. bipartita. However, the illustration of the anal papillae and anal valve of O. bipartita shows a greater similarity to the truncated posterior end of the bicornis-group than to the tapered posterior end of the limacina-group. There is no record of the presence of glandular ridges.

In his description of O. dannevigi, Benham (1916) stated that the last three segments of the body decrease in diameter successively and abruptly so that, from the side, they appear to be telescoped into one another, with a projecting posterior angle. This fact alone places O. dannevigi in the bicornis-group. The exact location of the origin of the ventral groove is difficult to ascertain. Benham observed that the ventral groove is, "at first narrowed, it attains its full width at about the tenth segment". If the ventral groove

originates at the anterior end of setiger 10, then the first abdominal segment (setiger 10) is abranchiate in this specimen (see Table I).

Discussion. The body formula devised by Tebble (1952) is a useful means of indicating the number and relationships between the branchiate and abranchiate segments in species of Ophelia. However, the use of the number of prebranchial segments as a major "dichotomy" in a key to the species, without including additional morphological characters, is impractical. For example, the body formula is based on the number and location of the branchiate segments. If, as in O. bicornis, the number of branchial segments is variable, then the body formula is also variable. The variation in the species may exceed the capabilities of the key. The third step in Tebble's(1953) key gives three choices; 8,9, or 10 anterior abranchiate setigers. Some specimens of O. bicornis from the same population (Griffith Head, Georgetown Island, Maine), have 11 or 12 anterior abranchiate setigers. Since there are no other morphological characters included in the key, it is impossible to determine the identity of the species from the key alone. Tebble's key is misleading in that it gives false impression of morphological affinites between certain species. Step 5 in the key includes those species which have 9 anterior abranchiate setigers. Step 6 includes those species with 10 anterior abranchiate setigers. This implies that O. bicornis is more closely allied to O. limacina than it is to O. denticulata. In fact, O. bicornis is more

closely allied to O. denticulata (see Table I). A more workable key should include information on the shape of the posterior region, the identity of the setiger in which the ventral groove begins, and the location of the glandular ridges (if present), in addition to the use of the body formula. Although the body of preserved specimens may be swollen or deformed, the origin of the ventral groove can always be determined. There are no annuli in the ventral groove. The site of the last complete annulus of the thoracic region is the point of origin of the ventral groove.

Bellan (1964) placed O. radiata, O. radiata var. barquii and forms A,B, and C of O. radiata into synonomy with O. bicornis. Bellan based his decision on the location of the first pair of branchiae (setiger 11, 12, or 13) and the total number of branchiae. In making his decision, Bellan did not take into account any other morphological characters of the species in question.

A study of specimens of O. bicornis collected from a population located at Griffith Head, Georgetown Island, Maine and other specimens from the United States National Museum (catalogue number 484 from Massachusetts and catalogue number 4927 from Virginia) indicated that regardless of the variation in the number and location of branchial setigers, there is no variation in the location of the glandular ridges (setiger 9) or in the point of origin of the ventral groove (anterior end of setiger 10).

Four specimens of O. radiata which were collected in

Naples, Italy (United States National Museum, catalogue number 5138) have glandular ridges located on setiger 10 and the ventral groove begins at the anterior end of setiger 11 (see table I).

Since there is a difference between the two species in the origin of the ventral groove and the location of the glandular ridges, I feel that O. bicornis and O. radiata should be considered separate species.

# SECTION V

## INTERNAL ANATOMY

## CIRCULATORY SYSTEM

Blood Sinuses. Extensive, voluminous perivisceral blood sinuses almost completely surround the esophagus, stomach, intestine, and rectum. Only the pharynx lacks a blood sinus. The blood sinuses, are connected in such a way that a continuous tube containing blood is formed around almost the length of the gut. Where a ventral typhlosole is present in the gut, the typhlosolar blood sinus connects to the perivisceral sinus along all or part of its length. The perivisceral blood sinuses reach their greatest development in the intestinal region.

Basically, the wall of the blood sinus is composed of an outer peritoneal covering, a layer of circular and/or diagonal muscle fibers, and an endothelial lining. The relative thickness of these layers varies in different regions of the digestive canal. In all regions, strands of connective tissue containing muscle fibers run through the sinus cavity between the outer and inner walls of the sinus. The muscle layer in the outer wall is composed of separate, apparently non-anastomosing fibers. The relationship of these fibers to the peritoneal covering is not clear. Since the fibers do not form a continuous sheet of tissue and no nuclei could be detected in these fibers, it is possible that each fiber may

be a part of the peritoneal cell (Hanson, 1949).

Starting at the junction of the pharynx and the esophagus, the esophageal blood sinus completely surrounds the esophagus. The peritoneal cells are only slightly modified resulting in a very thin covering over the sinus. The endothelial lining is composed of a thin, reticular network of cells. The sinus is more voluminous in the anterior region of the esophagus. Toward the posterior end, parts of the sinus become narrower and it becomes connected to the gut epithelium by a layer of connective tissue.

Near the junction of the esophagus and the stomach, in the region of the sixth setigerous segment, the midventral wall of the esophagus begins to fold inward toward the lumen of the gut. This fold is the beginning of the gastric typhlosole. The medial branch of the anterior ventral vessel is drawn into this fold. The two lateral branches of the anterior ventral vessel join and then empty into the perivisceral blood sinus. The sinus now completely surrounds the stomach but remains separate from the typhlosolar blood supply. As the stomach wall becomes more folded posteriorly, the remnants of the medial branch of the anterior ventral vessel become joined to the typhlosolar walls and eventually empty into the posterior ventral vessel through the typhlosolar vessels. The perivisceral sinus opens into the space enclosed by the typhlosolar walls (typhlosolar coelom), which is isolated from the perivisceral coelom (fig. 19). A major branch of the dorsal segmental vessel opens into the ventral

part of the perivisceral sinus in the region of the sixth setigerous segment (see detail below).

Toward the posterior end of the stomach (setiger 8), the sinus widens midventrally and a vertical layer of connective tissue forms which will eventually separate a small midventral cavity from the rest of the perivisceral sinus. It is within this small cavity that the two circumgastric vessels meet to form the subintestinal ventral vessel (fig. 20 ).

The composition of the wall of the gastric sinus is essentially the same as that of the esophageal sinus. In some specimens it has been observed that the peritoneal covering has become thicker but in others it remains thin. The muscle fibers, although mostly circular, are also arranged diagonally. With the exception of the pharynx, the muscle layers attain their greatest development in the wall of the stomach.

At the junction of the stomach and the intestine (between setiger 9 and 10) a middorsal evagination of the perivisceral sinus results in the formation of the heart. Ventrally, the vertical walls of the typhlosole converge but do not meet. A connective tissue layer separates away from the left and right typhlosolar walls cutting the posterior part of the typhlosole off from the perivisceral sinus. Another layer of tissue, originating from the typhlosolar epidermis, establishes the typhlosolar sinus in the dorsal part of the gastric typhlosole and then runs ventrally where it encircles the subintestinal ventral blood vessel (fig. 12 ).

At this point the typhlosole is open to the coelom. In mature males, the sperm actually enter the posterior part of the typhlosole through this opening. A pair of small blood vessels also pass through this opening and connect the posterior part of the gastric typhlosolar sinus to the subgastric extension of the ventral blood vessel. The gastric typhlosole separates from the ventral wall of the anterior part of the intestine. The blind pouch of the gastric typhlosole projects into the anterior part of the intestine in the region of the tenth setigerous segment (fig. 14).

At the beginning of the intestine, the perivisceral sinus expands and becomes very voluminous, reaching its greatest development. Also the peritoneal covering of the perivisceral sinus becomes thickest being modified into a thick layer of chloragogen tissue. The other layers of the sinus wall remain quite thin. The muscle layer consists of mostly scattered circular fibers. The endothelial layer is composed of cells with long processes which occasionally traverse the sinus.

The intestinal typhlosole begins in the anterior part of the intestine as a small inward folding of the ventral intestinal wall. At first, the typhlosole is filled with connective tissue but more posteriorly (setiger 12) the connective tissue disappears from the left side opening up the typhlosolar sinus to the perivisceral sinus, Although the right side of the intestinal typhlosole never opens up to the perivisceral sinus, the typhlosolar sinus remains in

contact with the perivisceral sinus through the opening in the left side along the whole length of the intestine. The intestinal typhlosolar sinus does not connect directly to the gastric typhlosolar sinus.

The rectal perivisceral sinus, which is nothing more than a continuation of the intestinal perivisceral sinus, begins at the anterior border of the first postbranchial segment (setiger 28) and continues to the last setigerous segment (32). Within the rectum, the typhlosole gradually changes to the anal valve. The sinus within the typhlosole is continuous with the rectal perivisceral sinus. Extensions of the sinus are found in the anal valve and anal valve papillae.

The cellular composition of the sinus wall in the postbranchial (rectal) region is quite different from that in the branchial (intestinal) region. The thick covering of chloragogen cells ceases abruptly at the anterior margin of the first postbranchial segment. The outer wall of the perivisceral rectal sinus is covered by a thin layer of peritoneum, a layer of circular muscle fibers, and a thick connective tissue layer which is continuous with the septa. The inner layer is a relatively thick layer of endothelial cells which have processes that cross the sinus space and connect to the basement membrane of the gut cells.

Heart. The heart is a middorsal evagination of the perivisceral sinus at the junction of the stomach and the intestine (fig. 9 ). It extends anteriorly over the stomach

and remains completely free from the sinus which surrounds the stomach. In diastole, the heart is as broad as the stomach posteriorly and becomes narrower at its anterior end. Schaeppi (1894) refers to it as pear-shaped.

The wall of the heart, being a continuation of the wall of the perivisceral sinus, has basically the same composition as that of the sinus. The most noticeable difference is in the muscle layer. The circular muscle bands, though still not forming a continuous sheet of tissue, become still thicker and more compact. The muscle bands appear to be thickest at the base (posterior end) of the heart near the sinus. No longitudinal muscle fibers have been seen. Although the muscle fibers are relatively thick, the overall thickness of the wall of the heart is no thicker than 0.01 mm. By way of comparision, the height of a single cell in the wall of the intestine of the same specimen is 0.044 mm. The endothelial lining of the heart is present but only as a very thin layer. This layer has been observed only in tangential sections of the heart.

Within the heart, a cylindrical structure, called the heart body by Schaeppi (1894), is tightly appressed to the ventral wall. A strand of connective tissue connects the posterior end of the heart body to the basement membrane of the cells lining the dorsal wall of the intestine (fig. 30 ). At the anterior end of the heart, the heart body becomes expanded or club shaped. It is composed of elongated flattened cells whose membranes have become modified into long, fibrous processes. These cells are scattered through a clear, homogeneous

supporting matrix. The cellular composition of the heart body appears to be similiar in some respects to that of vertebrate cartilage (fig. 29 ).

Blood Vessels. Two large, lateral branches arise from the anterior end of the heart and angle posteriorly and ventrally around each side of the stomach (see below).

The dorsal blood vessel also originates at the anterior end of the heart and from there it runs anteriorly, passing through the septa of the injector organ (see muscular system) as far as the brain. The structure of the wall of the dorsal blood vessel changes as it passes through different areas of the anterior region of the body. Near the heart, the dorsal blood vessel is relatively thick walled, with a thin covering of peritoneum, a layer of circular muscle fibers, and a relatively thick endothelial lining. In addition, the ventral surface of the vessel has four groups of longitudinal muscle bands lying between the peritoneal layer and the circular muscle layer. One of these groups of longitudinal muscle fibers attaches to the dorsal wall of the stomach. As the dorsal blood vessel passes through the septa of the injector organ, it becomes surrounded by a thick layer of longitudinal muscle bands. Anterior to the injector organ the dorsal blood vessel becomes very thin walled and attached to the dorsal body wall by a mesentery.

Posterior to the injector organ the dorsal blood vessel gives off pairs of dorsal segmental blood vessels which go to the setal sacs of the sixth, fifth, and fourth

setigerous segments (see segmental blood vessels). As soon as the dorsal blood vessel has passed through the outer septum of the injector organ it gives off a pair of dorsal segmental vessels which travel anteriorly to the setal sacs of the third setigerous segment. The setal sacs are located on the lateral body wall between the outer and inner (posterior and anterior) injector organ septa. The dorsal segmental blood vessels are attached by a membrane to the anterior face of the outer septum. Both the dorsal blood vessel and the dorsal segmental blood vessels give off many small, blind-ending branches which nearly fill the space between the two septa.

After passing through the inner septum of the injector organ the dorsal blood vessel gives off another pair of dorsal segmental blood vessels which run along the anterior face of the septum to the setal sacs of the second setigerous segment. These branches give off many more blind vessels than does the preceding pair of dorsal segmental vessels.

When inverted the highly folded pharynx fills the coelom enclosed by the anterior part of the inner septum. The dorsal blood vessel, which is attached to the dorsal body wall by a mesentery, runs anteriorly between the two major longitudinal folds of the pharynx. Many blind blood vessels which branch off the dorsal blood vessel lie in the fold of the pharynx. When the pharynx is everted the blind vessels protude into the coelomic space between the walls of the pharynx.

There are no segmental blood vessels directly assoc-

iated with the setal sacs of the first setigerous segment. Anterior to the mouth, a complex of blood vessels is formed composed of a pair of branches of the dorsal blood vessel, the two branches of the ventral blood vessel, and a cross connection between the two ventral blood vessels (fig. 9 ). The branches of the paired dorsal blood vessels connect with the two ventral blood vessels. At this point of attachment, two more pairs of blood vessels are given off. One pair goes dorsally and gives off blind branches which lie close to the pharynx. The other pair of blood vessels travels to the coelomic space lateral to the oblique muscles and then continues anteriorly almost to the brain. Numerous blind vessel branches are derived from these vessels along their whole length.

Anterior to the vascular complex described above, the dorsal blood vessel gives off a pair of vessels which attach to the ventral blood vessels. There is a short cross connection between the two branches of the dorsal blood vessel.

The dorsal blood vessel continues anteriorly in the dorsal part of the coelom and, upon reaching the brain, bends ventrally and ends blindly beneath the brain. Slightly before reaching the brain, the ventral blood vessels originate as a pair of branches of the dorsal blood vessel. The ventral blood vessels remain close together and slightly ventral to the dorsal blood vessel as far back as the anterior lip of the mouth. At this point they receive the branches of the dorsal blood vessel and contribute to the vascular complex described above. At the anterior lip of the mouth the ventral blood

vessels diverge, pass ventral to a large transverse muscle band, and then pass ventral to the corners of the mouth. When passing lateral to the mouth, the ventral blood vessels follow a course similar to that of the circumpharyngeal connectives but remain medial to the oblique muscles which attach to the corners of the mouth. Posterior to the mouth, the ventral blood vessels are situated directly over the subpharyngeal ganglion. In the region of the subpharyngeal ganglion (setiger 3) all of the major blood vessels are enclosed within the inner septum of the injector organ.

The ventral segmental blood vessel, which connects directly to the dorsal segmental vessel near the setal sacs of setiger 2, runs along the anterior face of the inner (anterior) septum of the injector organ and connects to the ventral blood vessel in setiger 3.

The two branches of the ventral blood vessel converge and fuse prior to passing through the inner septum (setiger 4). Soon after passing through the septum, the ventral blood vessel receives the ventral segmental blood vessel branches associated with the setal sacs of the third setigerous segment. As in the preceeding segment, the dorsal segmental blood vessel connects to the ventral segmental blood vessel near the setal sac. Both pairs of ventral segmental blood vessels are held in position by a membrane which is attached to the anterior wall of the septum with which the blood vessel is associated. Also, both pairs of ventral segmental blood vessels give off many blind ending branches which lie within the spaces enclosed

by the septa of the injector organ.

The ventral blood vessel passes through the ventral wall of the outer injector organ septum and immediately divides into three branches. Posterior to the injector organ and beneath the esophagus the two lateral branches of the ventral blood vessel receive the ventral segmental blood vessel associated with the setal sacs of setigers 4 and 5 respectively (fig. 9 ).

Near the posterior end of the esophagus the two lateral branches of the ventral blood vessel blend into the esophageal blood sinus. At this point, the gastric typhlosole is just beginning to form as an infolding of the midventral wall of the gut. As the infolding takes place, the medial branch of the ventral blood vessel is drawn up into the typhlosole and becomes continuous with the typhlosolar circulation of the stomach (figs. 15-18).

Dorsal to the anterior half of the stomach, a pair of lateral, contractile loops of the heart, the circumgastric vessels, originate at the anterior end of the heart. From their point of origin, the circumgastric vessels descend posteriorly and ventrally around each side of the stomach, converge in the ventral midline, and fuse beneath the junction of the stomach and the intestine forming the subintestinal ventral blood vessel and two short, parallel, blind-ending subgastric extensions. In addition to the peritoneal and muscle layers,the wall of the circumgastric vessels has a relatively thick endothelial lining. In serial sections,

some of the endothelial cells appear to slough off and become free in the blood.

The subgastric vessels run parallel to each other toward the anterior part of the stomach where, near the end of setiger 7, they are connected to the ventral wall of the stomach by two strands of connective tissue containing relatively thick longitudinal muscle fibers. Branches of the subgastric vessels include ventral segmental blood vessels which go to the setal sacs of setigers 8, 9, and 10 and a single pair of typhlosolar blood vessels (fig. 9 ). The pair of typhlosolar vessels originate in the two pouches of the gastric typhlosole that extend into the anterior part of the intestine. The vessels run ventrally out of the typhlosole, curve anteriorly on either side of the subintestinal ventral blood vessel and join the subgastric vessels immediately anterior to the point where the two circumgastric vessels join. The anteriormost pair of ventral segmental blood vessels runs laterally to the setal sacs of setiger 8. The following two pairs of vessels go to setigers 9 and 10 respectively. At the setal sac, each of the three pairs of vessels gives rise to a branch, the intersegmental vessel, which runs posteriorly to the setal sac of the following segment where it breaks up into many blind vessels. Along its course, the intersegmental blood vessel gives rise to branches which appear to end blindly in the ventrolateral longitudinal muscle bands. Near the setal sac, where the ventral segmental vessels give rise to the intersegmental

vessels, a small branch runs dorsally to the dorsolateral body wall. The ventral segmental blood vessels which go to the setal sacs of setiger 10 pass into the first pair of branchiae (see branchial circulation).

The pair of ventral segmental blood vessels which go to the setal sacs of setiger 7 arise at the base of the circumgastric vessels and run diagonally to the setal sac (fig. 9 ). The intersegmental blood vessel and its branches are similar to those described for setigers 8 and 9. Thick longitudinal muscle bands run the length of this ventral segmental vessel in a loose spiral arrangement.

The subintestinal ventral vessel, formed by the union of the two circumgastric vessels, extends from its point of origin to the end of the last setigerous segment (setiger 10 to 32) where it bifurcates, sending a branch to each of the large ventral anal papillae. The subintestinal ventral vessel is enclosed in the midventral groove caused by the infolding of the intestinal typhlosole by a pair of connective tissue membranes. There is no evidence that the subintestinal vessel has any openings into either the intestinal sinus or the typhlosolar sinus. There are a few minute middorsal openings in the subintestinal ventral vessel which allow some blood to pass into a layer of connective tissue which separates the typhlosolar sinus from the subintestinal ventral vessel. However, the blood does not appear to enter the sinuses.

The subintestinal ventral vessel is very thin walled and is composed of a thin peritoneal covering, minute circular

muscle fibers, and lined with scattered, reticular endothelial cells.

Segmental blood vessels branch off the subintestinal ventral vessel in every setigerous segment of the branchial and postbranchial regions. In the branchial region, each vessel (afferent branchial) runs laterally to the body wall and, passing through a thin membrane, enters a gill. In the postbranchial region, each vessel runs laterally in close association with the anterior septum of the segment and connects to a corresponding dorsal segmental vessel near the setal sac.

Intersegmental blood vessels, each derived from a ventral segmental blood vessel, run from the setal sac of one segment to that of the following segment in each of the segments of the branchial region and in all but the last segment in the postbranchial region. Intersegmental blood vessels do not connect to each other but, instead, break up into a tuft of small blind-ending vessels as they approach the setal sac of the following segment (fig. 9).

The two branches of the subintestinal ventral vessel, which bifurcates at the posterior end of the last setigerous segment (setiger 32), widen in each internal segment of the ventral anal papillae. No connection between the subintestinal ventral vessel and the perivisceral or typhlosolar sinuses could be detected in either the postbranchial or the pygidial region.

Dorsal segmental vessels (efferent branchial) run

to the perivisceral sinus from the branchiae in each of the branchial segments and from the setal sacs in each of the postbranchial segments. In the anterior part of the branchial region, each of the pairs of dorsal segmental vessels leaves the sinus near the dorsal midline as a single, tubular vessel which is not supported by a membrane. Toward the posterior end of the branchial region (near setiger 21), a membrane attaches the dorsal segmental vessel to the outer wall of the intestinal sinus. In each succeeding segment, the membrane supports more of the blood vessel. As the supporting membrane becomes more extensive, more of the blood vessel becomes incorporated into the membrane and there are more connections between the blood vessel and the perivisceral sinus. The dorsal segmental vessel of the last branchial segment (setiger 27), for example, opens to the intestinal blood sinus through many channels in the membrane. The dorsal segmental vessels of the postbranchial region are incorporated into the anterior septa of each segment (see segmental circulation for detail).

Segmental Circulation. In a dissection of an anesthetized specimen of Ophelia denticulata, the most striking anatomical feature in the prebranchial region is the heart. Another prominent feature is the abundance of small blind blood vessels which appear to nearly fill the coelom posterior to the heart.

The segmentally repetitive arrangement of blood vessels has been modified in the region of the heart, injector organ

septa, and eversible pharynx. However, the fourth setigerous segment probably is as close to the unmodified condition as any. Here a dorsal segmental vessel runs from the dorsal vessel to the setal sac where it connects to the ventral segmental vessel, which is a branch of the lateral member of the three branches of the ventral vessel. The intersegmental vessel runs posteriorly to the setal sac of the fifth setigerous segment. Branches of the intersegmental vessel end blindly in the longitudinal muscle bands of the ventrolateral body wall. The posterior end of the intersegmental vessel breaks up into many blind vessels near the setal sac. At the anterior end of the intersegmental vessel, near the junction of the dorsal and ventral segmental vessels, a branch is given off which runs to the longitudinal muscle bands of the dorsolateral body wall. This branch rebranches repeatedly. The secondary branches either end blindly in the coelom near the body wall or form a loop around a muscle band and rejoin the vessel from which it originally branched. Both the dorsal and ventral segmental vessels give off secondary branches which rebranch and eventually end blindly in the coelom. The blind branches of the dorsal segmental vessel nearly fill the dorsal part of the coelom immediately posterior to the injector organ septa. The branches of the ventral segmental vessel either go to longitudinal muscle groups or lie free in the coelom. Some branches run laterally in the segment and others run in an anterior or posterior direction in the same segment or into the following segment.

There are no intersegmental vessels in the segments anterior to the injector organ septa (setigers 1, 2, and 3). The branches anterior to the mouth serve mainly to connect the dorsal vessel to the ventral vessel. The arrangement of vessels in setiger 5 is similar to that of setiger 4.

Setigerous segments 7, 8, and 9 differ from the fourth in that there are no dorsal segmental vessels. Here the circulation to the body wall is supplied by the ventral segmental vessels and the branches of the intersegmental vessels. Setigerous segment 6 is similar to the fourth except that the ventral segmental vessel connects to the middle of the dorsal segmental vessel rather than connecting with the dorsal segmental vessel at the setal sac. The ventral segmental vessel enters the blood sinus at the anterior end of the stomach rather than connecting to the ventral vessel.

The segmental branches in each of the segments of branchial region are very similar. Each segment contains a pair of dorsal segmental vessels (efferent branchial), a ventral segmental vessel (afferent branchial), and an intersegmental vessel. The ventral segmental blood vessels and the intersegmental blood vessels give rise to many blind-ending branches. Any modification of these three blood vessels is the result of their association with the two types of nephridia found in the branchial region.

The dorsal and ventral segmental blood vessels (branchial vessels) of the first branchial segment (setiger 10)

are not associated with nephridia. The dorsal segmental vessel (efferent branchial) runs ventrally from the dorsal part of the intestinal sinus, passes between the oblique muscle bands, and enters the gill through a small opening in the body wall dorsal to the notopodial setal sac. A thin membrane partially closes off the opening to the coelom but coelomic fluid, coelomocytes, and gametes can be found in the lumen of the gill. The ventral segmental blood vessel (afferent branchial) extends laterally and posteriorly from the subgastric extension of the subintestinal ventral vessel and enters the same opening to the gill as does the dorsal segmental vessel. Prior to entering the gill, the ventral segmental blood vessel gives off the intersegmental blood vessel, which runs beneath the oblique muscles to the setal sac of setiger 11. This vessel gives off many blind branches which nearly fill the ventrolateral coelom beneath the oblique muscles.

The dorsal and ventral segmental vessels (branchial blood vessels) extend in the coelom of the branchiae, to the tip. A series of capillaries, lying in deep grooves in the thick epidermis, encircle the branchiae and connect the two branchial blood vessels at regular intervals along the entire length (see branchiae). The branchial vessels do not appear to be connected at their distal extremities.

A pair of nephridia occurs in each of the following six segments (setigers 11 to 16). The ciliated nephrostome of the nephridia, which remains dorsal to the oblique muscle

bands, attaches to both the dorsal and ventral segmental vessels (fig.43) (see excretory system). Folds of the nephrostome grow around the blood vessels. Small openings between the blood vessels and the expanded sinus-like walls of the nephrostome allow blood to enter. In serial section, it appears that the blood from the two vessels may mix in the nephrostome walls. The two blood vessels run ventrolaterally along both sides of the wall of the nephrostome and, near the lateral body wall, the blood vessels enter the opening into the branchiae. The nephridial tubule turns posteriorly, runs along the ventrolateral body wall, and empties to the outside through a nephridiopore located anterior to the setal sacs of the following segment.

The intersegmental vessels, which are branches of the ventral segmental vessel, follow along the dorsal side of the nephridial tubule. Blind vessels branch off along the whole length of this vessel. Some of the blind branches may run dorsally between the oblique muscle bands and end in a tuft near the nephrostome. Other blind branches may turn anteriorly from their point of origin and nearly fill the ventrolateral coelom beneath the oblique muscles.

No branches are given off the dorsal segmental vessels. Branches of the ventral segmental vessels are variable. They tend to increase in number in the posterior segments. The branches remain dorsal to the oblique muscles, some running to the dorsolateral longitudinal muscle bands, and others may pass beneath the ventral nerve cord. Those branches

going to the muscle bands or beneath the ventral nerve cord do not appear to anastomose with other blood vessels. If any connection is made to a blood vessel, it is usually to the same vessel from which it originally branched. The branchial blood vessels and the arrangement of the capillaries connecting them are the same throughout the branchial region.

The blood vessels of the remaining segments of the branchial region (setiger 17-27), though basically similiar to those of the preceding branchial segments, become somewhat modified because of their association with a different type of nephridium (see excretory system). The dorsal segmental vessel runs from the dorsal part of the intestinal sinus to the branchiae without connecting to the nephridium. The ventral segmental vessel and the nephridium join together beneath the intestine and remain in close association up to the point where the vessel enters the branchia. Although the nephridium almost envelopes the blood vessel, no blood actually enters the wall of the nephrostome as it does in the anterior pairs of nephridia. The intersegmental vessel branches from the ventral segmental vessel and then runs posteriorly along the dorsal side of the nephridial tubule. As in the preceding branchial segments, the blind branches of the intersegmental vessel nearly fill the ventrolateral coelom.

Supporting membranes attaching the dorsal segmental vessels to the sinus wall are found from the tenth to the last (eighteenth) branchial segment. Blood channels within the supporting membranes are first found in the thirteenth

branchial segment and become most extensively developed in the last branchial and first postbranchial segments. Also, a membrane connects the lateral side of the dorsal segmental vessel to the longitudinal muscles of the lateral body wall. The lateral membrane begins at about the middle of the dorsal segmental vessel and remains attached to the vessel up to the point where the vessel enters the branchia. There are no blood channels within the lateral supporting membranes.

Branches of the ventral segmental vessel give rise to blind vessels which usually remain beneath the intestine. Some branches run either anteriorly or posteriorly from their origin and come in contact with branches from adjacent ventral segmental vessels. No anastomoses between the small vessels could be detected by dissection or in serial sections. In the more posterior segments of the branchial region, more than one branch is given off the ventral vessel. The major branch is the ventral segmental vessel; the minor branches give rise to blind vessels. One of the minor branches in the last branchial segment runs dorsally and gives rise to many blind vessels which are situated in the dorsal coelom in the large space between the longitudinal muscle bands and the epidermis.

In the first postbranchial segment the dorsal segmental vessel originates from the lateral part of the intestinal sinus and is enclosed in the posterior septum of the segment. Near the setal sac, the dorsal segmental vessel leaves the septum and unites with the ventral segmental vessel. The ventral

segmental vessel gives off a branch, the intersegmental vessel, which turns posteriorly and extends to the setal sacs of the following segment where it breaks up into numerous blind vessels. Other blind vessels are given off along the whole length of the intersegmental vessel. The membrane which connects the dorsal segmental vessel to the intestinal sinus contains four or five major blood channels which open into the intestinal sinus.

In the following four postbranchial segments the dorsal segmental vessels originate at the ventrolateral wall of the rectal sinus where the septum attaches to the sinus wall. The vessel remains enclosed within the septum for a short distance and then becomes free of the septum. As in the first postbranchial segment, the dorsal segmental vessel joins the ventral segmental vessel near the setal sac. An intersegmental vessel, with its associated blind branches, is found in all but the last postbranchial segment.

The ventral blood vessel bifurcates at the posterior end of the last postbranchial segment, a branch going to each of the ventral anal papillae. The vessel becomes so dilated that it nearly fills each of the spaces in the internally segmented ventral anal papillae.

Blood Flow. The following description of the direction of the flow of blood in Ophelia denticulata is based on observations of dissected, living specimens and upon information obtained from a study of serial sections. Since Ophelia denticulata is a relatively large opheliid with a fairly

opaque body wall, observations on living, undissected specimens were of little value. Upon injecting a diluted suspension of India ink (Bell, 1947) into the intestinal sinus, the path taken by the blood in most of the prebranchial region was observed. However with the exception of the direction of blood flow in the intestinal sinus, no conclusive observations on the direction of the flow of blood in the branchial and postbranchial regions could be made. The major problems encountered were the occurence of a frequent reversal of flow in the dorsal segmental vessels; also, the general lack of capillary beds except in the branchiae makes it difficult to determine the afferent and efferent vessels.

An explanation of the direction of blood flow can not be made without two basic assumptions. First, it is assumed that blood flows in both directions in all blind ending vessels. Second, because no connection between the subintestinal ventral blood vessel and the intestinal sinus was found, it is assumed that blood flows from the subintestinal vessel through the ventral segmented vessels into the dorsal segmental vessels, and then into the intestinal sinus.

The relaxation of the heart muscles allows the heart to expand and to draw blood from the enlarged anterior portion of the intestinal sinus. Blood flows posteriorly in the perivisceral sinuses of the esophagus and the stomach and anteriorly in the intestinal sinus to replace the blood that was removed by the heart. The flow of blood in the sinuses is aided by contractions of the sinus wall. During the systolic

contraction, the wall of the heart squeezes tightly around the heart body causing the blood to be pushed anteriorly in advance of the wave of contraction. As the heart is contracting, the blood is forced out of the heart into the dorsal vessel and the circumgastric vessels. When the wave of contraction nears the anterior end of the heart, the heart body becomes pushed ahead so that its flared end blocks the opening into the dorsal vessel causing the remainder of the blood to flow into the circumgastric vessels. As soon as the heart has emptied, a wave of contraction begins in the dorsal part of the circumgastric vessels and proceeds along the whole length of these vessels. At the same time the blood is forced anteriorly as far as the brain in the contractile dorsal vessel. A cylindrical structure which is found in the posterior end of the dorsal vessel is histologically similar to the heart body. This structure in the dorsal vessel may aid in preventing a back flow of blood into the heart or circumgastric vessels when the contraction is first beginning in the dorsal vessel.

Blood flows from the dorsal vessel into the dorsal segmental vessels (afferent podial vessels) of setigers 2-6. In each of these segments, the blood flows from the dorsal segmental vessels into the ventral segmental vessels (efferent podial vessels) which then conduct the blood to the anterior ventral blood vessel or, in the case of the ventral segmental vessel of setiger 6, to the gastric sinus.

Blood also flows into the blind branches associated

with both the dorsal segmental vessels, the ventral segmental vessels, and the intersegmental vessels, where present, when pressure is high in the system. As the smaller blind ending vessels, which are free in the coelom, become filled with blood, it is possible to observe their expansion and waving movements. It is also possible to observe contractions in these vessels as they empty. As pressure decreases in the system, the contractions of the blind vessels and the elasticity of the intersegmental vessels return blood to both the dorsal and ventral segmental blood vessels. Some mixing of blood must occur because some of the blood which returns to the dorsal segmental vessel from the blind vessels must re-enter the blind vessels along with the "fresh" blood when pressure increases in the system again.

As mentioned previously, the blood flows anteriorly in the dorsal vessel as far as the brain and then enters the two branches of the anterior ventral vessel. Blood flows posteriorly in the anterior ventral vessel. Along their course, the anterior ventral blood vessels receive blood from the ventral segmental vessels of setiger 2 through 5. After passing through the inner septum of the injector organ, the two anterior ventral vessels join together and pass through the outer septum of the injector organ and then divide into three branches. At the junction of the esophagus and stomach, the blood from the two lateral branches of the ventral blood vessel enters the gastric sinus. The blood contained in the periesophageal sinus, the perigastric sinus, and that within

the typhlosole represent posterior flowing circulation.

There is no direct connection between the anterior ventral vessel and the subintestinal ventral vessel. Blood enters the subintestinal ventral vessel through the pair of circumgastric vessels from the heart. Blood also flows into the pair of subgastric ventral vessels and into the ventral segmental vessel which goes to the setal sacs of setiger 7. Blood from the subgastric ventral vessels flows into the ventral segmental vessels which go to the setal sacs of setigers 8, 9, and 10. From each of these vessels, blood flows into their associated intersegmental vessels and other blind vessels. Since there are no dorsal segmental vessels in the region of the heart in setiger 8 and 9, the blood must return to the subgastric vessels via the ventral segmental vessels.

Blood flow to setiger 7 is similiar to that in setigers 8 and 9. In setiger 10, however, blood flows from the subgastric ventral vessels to the first pair of branchia through the ventral segmental blood vessel (afferent branchial vessel). A series of small, transverse capillaries encircle the branchiae and connect the ventral segmental vessel (afferent branchial) to the dorsal segmental vessel (efferent branchial). Blood flows from the branchiae to the intestinal sinus. Throughout the branchial and postbranchial regions the blood flows posteriorly in the subintestinal ventral vessel and anteriorly in the intestinal sinus.

In the anterior segments of the branchial region

(setigers 9-16), blood flows into the nephrostomal sinuses between the walls of the nephrostome from both the dorsal and ventral segmental vessels. In serial cross sections, it appears that the nephrostomal sinuses form a connecting link between the dorsal and ventral segmental blood vessels. Therefore, the blood becomes mixed in the nephrostomal sinuses and it is possible that blood could flow from the ventral segmental vessel to the dorsal segmental vessel through the nephrostomal sinuses.

In the posterior part of the branchial region (setigers 17-27), the blood vessels are associated with a different type of nephridium (see excretory system). There is no blood sinus in the nephrostome and, although the nephridium is attached to the ventral segmental blood vessel, no blood enters the nephridium from the vessel. The only junction between the dorsal segmental vessel and the ventral segmental vessel is through the capillaries in the branchiae. Blood flows from the subintestinal ventral vessel to the branchiae through the ventral segmental vessels and from the branchiae to the intestinal sinus through the dorsal segmental vessels. In all of the branchial region, the intersegmental vessels and other blind branches of the ventral segmental vessels alternately fill and empty as pressure increases and decreases in the system.

Blood flow in the postbranchial region is essentially the same as that in the branchial region except that the blood flows directly to the dorsal segmental vessels from

the ventral segmental vessels. The two branches of the subintestinal ventral vessels, which end blindly in the ventral anal papillae, each carry blood which flows both in and out of the papillae.

Discussion. There are relatively few published accounts of the internal anatomy of members in the family Opheliidae. Of these, only the papers written by Claparède (1869), Schneider (1887), Schaeppi (1894), de Saint-Joseph (1898), Brown (1938), and Hartmann-Schröder (1958) are based on species of Ophelia. Schneider does not discuss the circulatory system of O. denticulata (as O. neglecta). Both de Saint-Joseph and Schaeppi state that the description of the circulatory system of O. radiata given by Claparède is inexact in many points. Hartmann-Schröder gives only a scanty account of the circulatory systems of the species of Ophelia that she studied, that is, O. rathkei, O. remanei, O. radiata, and O. limacina. She describes a basic pattern of the arrangement of the principle vessels of the opheliids and indicates how the species of Ophelia differ from this basic pattern. De Saint-Joseph stated that all details that Schaeppi gave on the circulation of the blood and on the cardiac body of O. radiata are applicable in O. denticulata (as O. neglecta). The most complete and detailed descriptions of the anatomy of the circulatory system of Ophelia are given by Schaeppi on O. radiata and by Brown on O. rathkei (as O. cluthensis). Basically, there is a great similarity between the anatomy of the circulatory system of O. radiata, O. rathkei,

and O. denticulata as described by Schaeppi, Brown, and myself. There are, however, some points of disagreement.

Schaeppi indicates that the dorsal vessel enters the palpode (Sinnespitz) and divides into two vessels which travel posteriorly. The two vessels rebranch and enter the injector organ. One pair of these branches enters the inner (anterior) sac and the other pair is located between the inner and outer sac of the injector organ. No vessels have been found in the palpode of O. denticulata. Instead, the dorsal vessel ends blindly beneath the brain. The two branches of the dorsal vessel that originate just posterior to the brain turn back and run posteriorly. They do not rebranch but continue into the inner sac of the injector organ as a single pair of blood vessels. However, before entering the injector organ, each branch of the ventral vessel receives the ventral segmental vessel that is associated with the setal sacs of setiger 2. Also the ventral segmental vessels associated with the setal sacs of setiger 3 run from the setal sac into the space between the two septa of the injector organ. These ventral segmental vessels do not join the anterior ventral vessel until it has passed through the outer septum of the injector organ. The location of the branches of the anterior ventral vessel as described by Schaeppi corresponds to the location of the ventral segmental vessels of setigers 3 and the branches of the anterior ventral vessel in O. denticulata. It is possible that the branches located between the inner and outer sacs that Schaeppi described as ventral vessels were the ventral segmental vessels coming

from the setal sacs of setiger 3.

Schaeppi also states that the anterior ventral vessel, soon after passing through the outer septum of the injector organ, divides into two branches. In O. denticulata the anterior ventral vessel divides into three branches. In both species, and also in O. rathkei according to Brown, the anterior ventral vessels connect with the perivisceral sinus at the junction of the stomach and the intestine but neither Schaeppi nor Brown describe the incorporation of a branch of the ventral vessel into the gastric typhlosole. It is the third or medial branch of the anterior ventral vessel which is incorporated into the gastric typhlosole in O. denticulata.

In O. denticulata, no unpaired branches of the dorsal vessel have been found near the outer septum of the injector organ as have been described by Schaeppi in O. radiata.

Schaeppi states that there is no extension of the posterior ventral blood vessel further forward than its junction with the circumgastric vessels. He does describe a group of four pairs of blind vessels, which originate from the the circumgastric vessels near their point of junction with the posterior ventral vessel. He does not indicate the destination of these vessels. Brown states that, in O. rathkei, the "contractile vessels" (i.e, circumgastric vessels) give off a number of small vessels to the body wall and to setal sacs of setigers 7 and 8. In O. denticulata, a pair of vessels extend forward under the stomach, from the junction of the

circumgastric vessels with the subintestinal ventral vessel. It is from this pair of subgastric ventral vessels that the ventral segmental vessels which go to the setal sacs of setigers 8, 9, and 10 originate. The fourth pair of ventral segmental vessels (to setal sac of setiger 7) originate at the point where the two circumgastric vessels unite.

It is evident that there is a basic similarity in the arrangement of blood vessels in the area beneath the stomach in all three species of Ophelia. But, it is difficult to determine whether or not the differences are the result of the author's interpretation of what he saw or are actually inherent differences between the species.

Schaeppi has observed, in O. radiata, anastomoses between the perivisceral sinus and subintestinal ventral vessel which give rise to the branchial artery and branchial vein in every branchial segment. The only anastomosis found in O. denticulata, other than in the branchiae, are found in setigers 11-16 where the blood can flow from the ventral segmental vessel through the nephridial sinus.

The greatest discrepancy between the description of O. radiata by Schaeppi and that of O. denticulata concerns the last few setigerous segments. Schaeppi states,

> Es liegt auf der Hand, das der Abdominal-sinus, streng genommen, auch nicht venöses, sondern gemischtes Blut mit vorwiegend venosun Character enthalt, denn dass Bauchgefass geht ja, wie wir noch nachholen müssen, im letzten Segments in der Darsinus über; indessen wird diese einmalig Zufuhr von gemischten Blut auf die Venosität des Darmsinusblutes Nur wenig Einfluss haben, und durfen wir daher diesen Faktor in einem Schema Verachlassigen.

Neither Brown (1938) nor Claparède (1869) mention whether or not such a union between the posterior ventral vessel and the perivisceral sinus exists in O. rathkei and O. radiata.

Hartmann-Schroder's observations appear to be in agreement with those of Schaeppi. In describing the anatomical structures of the circulatory system that all the genera of the Opheliidae have in common she states:

> Dieses ventrale Darmgefäss reicht nach hinten bis zum Ende des Mitteldarms, wo es in den grossen Darmblutsinus mündet, der den ganzen Mitteldarm bedeckt und auch das Herz mit Blut versorgt.

Although this does not refer specifically to the Ophelia species, she points out:

> Das Blutgefäss-System der Ophelia gruppe und von Travisia forbesii weicht kaum von dem eben gezeichneten Schema ab.

In O. denticulata, no junction between the posterior ventral vessel and the perivisceral sinus has been found. As will be discussed further below, the presence or absence of a direct connection in the posterior segments between the subintestinal ventral vessel and the perivisceral sinus has a great bearing on the direction of blood flow in the branchial and postbranchial regions.

The direction of blood flow in O. radiata, as described by Schaeppi, and that described above for O. denticulata is the same in all respects except one. This point of difference occurs in the description of the flow of blood in the dorsal

and ventral segmental vessels associated with the intestinal sinus and the subintestinal ventral vessel in the branchial and postbranchial regions. In O. radiata, according to Schaeppi, the blood flows into the dorsal segmental vessels from the intestinal sinus, and then flows from the dorsal segmental vessels to the ventral segmental vessels via the branchial capillaries. From the ventral segmental vessels the blood flows into the subintestinal ventral vessel. Blood flows back into the intestinal sinus from the subintestinal ventral vessel where they join together in the last few segments. Blood also enters the anterior end of the posterior ventral vessel by way of the circumgastric vessels.

Since no junction between the posterior ventral vessel and the intestinal sinus could be found in the posterior segments in O. denticulata, it would seem to be physically impossible to continually add blood to a blind subintestinal ventral vessel via the dorsal and ventral segmental vessels. In addition, one can observe the almost continual flow of blood from the heart to the posterior ventral vessel via the circumgastric vessels. Also, there would be no means of returning blood to the intestinal sinus if blood were to be removed from the sinus through the dorsal segmental vessels.

In O. denticulata, blood must flow from the posterior ventral vessel into the ventral segmental vessels and then to the intestinal sinus through the dorsal segmental vessels. In the branchial region, the ventral segmental vessels are the afferent branchial vessels and the dorsal segmental vessels

are the efferent branchial vessels.

In both O. radiata and O. denticulata, the only contact between the blood circulating in the prebranchial region and that circulating in the branchial and postbranchial regions occurs in the perivisceral sinus at the junction of the stomach and the intestine. Schaeppi points out that, since there are no branchiae in the anterior region, it would appear that this region is only supplied with venous (deoxygenated) blood. In addition, the blood from the intestinal sinus, which enters the "anterior" circulation by way of the heart is, according to Schaeppi, mixed and predominantly of a venous (deoxygenated) nature. However, he does not believe that the anterior region is supplied only with venous blood. Schaeppi suggests that it is possible that, in the highly folded wall of the stomach, the blood in the sinus undergoes oxygenation. The result is, according to Schaeppi, "An Stelle des arteriellen Bauchgefässes ist ein arterieller Darmsinus getreten" and the blood which enters the "anterior" circulation is at least partially oxygenated.

However, if one considers the physiological implications of the flow of blood as described for O. denticulata in which oxygenated blood enters the intestinal sinus through the dorsal segmental vessels (efferent branchial vessels) then the blood which enters the "anterior" circulation will be mixed because venous blood from the esophageal and gastric sinuses is added to the arterial blood of the intestinal sinus at the junction of the stomach and the intestine. If, as

Schaeppi suggests, the blood becomes oxygenated in the gastric sinus, then the blood which enters the "anterior" circulation would be wholly of an arterial nature.

There is the possibility that the exchange of gases could occur in sites other than in the branchiae and the folds of the stomach wall. McConnaughey and Fox (1949) described two large, thick walled, bent outfoldings from the gut, bearing longitudinal strips of especially strong, densely crowded cilia in the dorsal wall of the rectum of Euzonus (Thoracophelia) mucronata (Treadwell). Concerning these ciliated organs McConnaughey and Fox indicate that they probably serve a respiratory function. Two similiar structures occur in the dorsal wall of the rectum in O. denticulata. A third "ciliated organ" occurs in the anal valve (see digestive system).

The thin-walled proboscis of O. denticulata has a bright red color when everted and some blind vessels can be seen projecting into the space between the walls of the proboscis. Although the coelomic spaces between the walls of the proboscis becomes filled with coelomic fluid, the red color must be caused by blood since the coelomic fluid, is straw colored. The outer surface of the proboscis is is heavily ciliated. The beating of the cilia causes a flow of water around the proboscis. All of these factors lead one to believe that the proboscis may be involved in the transfer of gases to and from the blood.

The small, numerous blind vessels, the closed ends of

which lie free in the coelom, are evidently not restricted to the genus Ophelia. In addition to the reports by Claparède (1869) and Schaeppi (1894) of the occurence of blind vessels in O. radiata, McConnaughey and Fox (1949) have reported their occurence in Euzonus (Thoracophelia) mucronata. Blind vessels have also been found in the serpulids (Hanson, 1950a) and the sabellids (Hanson, 1950b). Fox (1938) has suggested that the blind capillaries which are found in the coelom of Sabella may aerate the coelomic fluid indirectly providing a supply of oxygen to the muscles. This may also occur in Ophelia and Euzonus.

## MUSCULATURE

General. The musculature of the body wall consists of three major layers, circular, longitudinal, and oblique. The circular layer of muscles is the outermost layer and is located between the basement membrane of the epidermis, where it is connected by strands of connective tissue, and the longitudinal layer of muscles.

The longitudinal muscle bands extend almost the whole length of the animal. They are absent in the lateral regions where the setal sacs are located, in the midventral region, and middorsally where they are either greatly reduced or absent. Thus they form four major groups; the dorsolateral and ventrolateral longitudinal muscle bands. The dorsolateral group extends from the dorsal midline laterally to slightly above the setal sacs. The ventrolateral group extends from

below the setal sacs almost to the ventral nerve cord (fig.19 ). The longitudinal muscle bands are attached to the body wall by a layer of connective tissue that is continuous with the basement membrane of the epidermis.

Except in the preoral region, the oblique muscles occur as paired bands which extend from just above the setal sacs to the ventrolateral body wall near the ventral nerve cord. Where the oblique muscles attach to the epidermal layer, cuticular invaginations enter the epidermis but do not completely pass through and the oblique muscle fibers attach to the cuticular invaginations (fig. 51 ). These cuticular invaginations, reminiscent of the apodemes of arthropods, are made readily visible in sagittal sections by the P.A.S. staining technique.

Prebranchial Region. No muscle layers have been found in the conical palpode. At the junction of the palpode and the annulated part of the prostomium, the ventrolateral group of longitudinal muscles and some thick bands of oblique muscles appear. The oblique muscles pass on either side of the brain and connect ventrally to the body wall, forming the two preoral grooves. Near the posterior part of the brain, thin circular muscles bands, interrupted by the oblique muscle bands, appear in the zone between the preoral grooves. The dorsal longitudinal muscle bands first appear slightly anterior to the nuchal organs and occur as an uninterrupted layer which extends along the dorsal surface between the two nuchal organs (fig.76). The circular muscle layer begins in

the dorsal and lateral areas posterior to the nuchal organs. As Rullier (1950) points out, the oblique muscle bands become attached to the base of the nuchal organs and, along with a transverse band of muscles which runs between the nuchal organs, serve as the retractor muscles for the nuchal organs.

In the area between the mouth and the nuchal organs, the oblique layer of muscles practically fills the coelom. The dorsal longitudinal muscles are formed into separate bands which appear rectangular in cross section.

The circular muscle bands are located in the area between the annuli. The oblique muscle bands attach dorsally and laterally in the intervals between the longitudinal muscle bands and run to the opposite side of the body and attach to the preoral groove. The bands from the left side of the body interdigitate with those of the right side (fig.77 ). Some oblique muscles extend from the middorsal line to the midventral line so that they, in actuality, are vertical muscle bands.

Immediately anterior to the mouth, a thick, transverse muscle band extends across the coelom immediately below the dorsolateral bands of longitudinal muscles. In the mouth region, oblique muscle bands attach to the corners of the mouth. Both the anterior and posterior lip are lined with tall, thick bands of circular muscles. All three muscle layers are present in the region just posterior to the mouth. However, the oblique muscle layer becomes reduced to narrow, widely spaced bands.

Two muscular modified septa, which occur posterior to the mouth, originate between setigers 2 and 3 and between setigers 3 and 4. They are modified into a conical, double-walled sac known as the injector organ. The anterior septum is enclosed within the posterior septum. The septa extend posteriorly from their point of origin and lie dorsal to the esophagus.

Each of the septa of the injector organ is composed of a thin layer of longitudinal and diagonal muscle fibers over a thick layer of circular fibers (fig. 15).

The action of the injector organ has been observed in some small living specimens. It was observed that the "head" of the worm did become more turgid upon contraction of the injector organ.

Near the end of the last segment of the prebranchial region (setiger 9), a pair of glandular ridges is located on the lateral body wall above the setal sacs. Oblique muscle bands extend from the upper and lower parts of the glandular ridge to the ventrolateral body wall. Thick circular muscle bands attach to the upper and lower parts of the glandular ridges causing them to bulge outward (fig. 31).

Branchial Region. In the first two segments of the branchial region (setigers 10-11), the oblique muscle bands become progressively thicker and the circular muscle bands become reduced in size (figs. 22,37,and38).

By the end of setiger 11, the pattern of the arrangement of the muscle layers has been established and will

continue throughout the branchial region. The oblique muscles occur in thick bands, usually five or six per segment. As seen in cross sections, each of these bands in turn is subdivided into five to nine vertically arranged bands. Beginning in setiger 13, the oblique muscle bands attach to the ventral body wall beneath the ventral nerve cord. In the more posterior segments of the branchial region, the upper pairs of the oblique muscle bands attach to a midventral projection of the cuticle and to an infolding of the basement membrane of epidermis (fig.23 ). The ventral nerve cord is moved upward by the oblique muscle bands.

The oblique muscle bands become interrupted at the end of the segment where the setal sacs occur. As a result of the increase in the number and size of the oblique muscle bands, the lateral and midventral part of the body, where the oblique muscle bands attach, become pulled inward. As has been pointed out by most of the investigators who have worked on the Opheliidae (Claparède, 1869; de Saint-Joseph, 1898; McIntosh, 1915; Tampi, 1959; McConnaughey and Fox, 1949), the deep, paired lateral grooves and the midventral groove, characteristic of most of the genera in the Opheliidae, is caused by the action of these strong oblique muscle bands.

The formation of the lateral and ventral grooves by the oblique muscle bands causes a division of the coelom into three compartments in the members of the genus Ophelia (fig.23). The upper compartment, in which the gut is located has been called the perivisceral coelom and each of the two lower

compartments have been called the nephridial coelom because the nephridial tubules are found there (Schaeppi, 1894).

The dorsolateral groups of longitudinal muscle bands are located in the perivisceral coelom. The ventrolateral groups of longitudinal muscle bands are located in the nephridial coelom. The longitudinal muscle bands reach their greatest development in the branchial region.

The longitudinal muscle bands lift away from the body wall in the posterior part of the last branchial segment. They reattach to the body wall at the junction of the last branchial and first postbranchial segment.

The circular muscle layer, occuring as individual fibers rather than in bundles, almost disappears. They are more numerous in the lateral body wall.

Postbranchial Region. The postbranchial region is the only region in which typical septa occur between the segments. Except for the one between the last branchial and first postbranchial segments, the septa are complete. This first septum is united to the lateral and medial parts of the dorsal segmental vessel which goes to the branchiae of the last branchial segment but does not extend to the dorsal body wall. Ventrally, the septa at the anterior and posterior ends of the first postbranchial segment are quite thick and contain numerous fibers. The muscle fibers extend upward into the gut and attach to the inner part of the typhlosole. It appears that these septa serve two functions, that of anchoring the gut to the body wall, and causing the lateral movements

of the anal valve. The muscle fibers may also act as retractors of the anal valve.

The septa of the remaining four segments are double walled sheets of connective tissue that are continuous with the basement membrane of the epidermis and the outer wall of the rectal blood sinus (fig.41 ). Individual muscle fibers, running parallel to the face of the septum, are found on both the anterior and posterior face of the septum. An extremely thin layer of peritoneum covers the muscle bands. These muscle bands, where the septum covers the rectal sinus, constitute the circular muscle layer of the sinus wall.

The muscle layers of the body wall in the postbranchial region become greatly modified. The longitudinal muscle bands become reduced in size and number. At the anterior end of the first postbranchial segment, the dorsolateral longitudinal muscle bands separate from the body wall, run posteriorly, and attach to the middle of the septum at the posterior end of the segment (fig.42 ). The thin longitudinal muscle bands remain separated from the body wall. The only point where the longitudinal muscle bands come close to the epidermal layer is at the junction of two adjacent segments. The longitudinal muscles extend as far back as the end of the postbranchial region.

The circular muscle fibers are more evident in the postbranchial segments than in the branchial segments because longitudinal muscle bands have separated away from the body wall. The circular muscle layer becomes quite thick in the

dorsal and dorsolateral wall of the last two postbranchial segments. This layer becomes continuous with the oblique muscles and, in the last postbranchial segment, the circular and oblique muscle layers fill the coelomic space between the rectum and the body wall (fig.25 ). In the posterior part of the last postbranchial segment, the circular muscles connect to the rectal wall (fig.25 ). The oblique muscle layer is strongly developed in each of the postbranchial segments.

The portion of the pygidial segment anterior to the anal papillae is divided internally by septa into seven compartments. Each of the compartments is nearly filled with thick circular muscle bands which attach to the septa. The appearance of septa in the pygidium suggest the possibility that the pygidial segment may be composed of a number of fused segments (possibly 7-8).

The two ventral anal papillae are also internally divided by septa. There are six major compartments (segments) near the expanded base of the ventral papillae and numerous, thin septa occur in the distal end of these papillae. There are circular, longitudinal, vertical and oblique bands in the ventral anal papillae. The vertical bands achieve the greatest development.

Setal Sacs. In the prebranchial region, the setal sacs have basically two sets of protractor muscles. One set attaches to the innermost or medial part of both the noto- and neuropodial sacs. The other set attaches to the end of the setal sacs nearest the cuticle (lateral end) (fig.32 ).

In the set attached to the medial end of the setal sac, there are usually three long muscle bands which run anteriorly and three which run posteriorly at an oblique angle, one muscle band runs dorsally, and another ventrally to the body wall. In the second set, there are usually three or four short muscle bands which run dorsally from the notopodial setal sac and ventrally from the neuropodial setal sac to the body wall (fig. 32 ).

There is a single retractor muscle which attaches to the noto- and neuropodial setal sacs and also attaches to the base of the lateral organ. This retractor muscle extends from the setal sacs to the ventrolateral body wall near the ventral nerve cord (fig. 31 ).

Three thick muscle bands attach to the adjacent walls of noto- and neuropodial setal sacs. One band attaches to the lateral ends of the setal sacs, another attaches the two medial ends, a third muscle band runs diagonally between the medial and lateral ends of the setal sac.

The arrangement of the protractor and retractor muscle bands in the setal sacs of the branchial region is similiar to that of the prebranchial region. However, the muscle bands are usually shorter because the setal sacs are located in an outpocketing of the body wall and the muscle bands attach to the walls of the pocket (fig. 34 ).

Proboscis. The retracted proboscis becomes folded into two major longitudinal folds with a deep longitudinal, middorsal groove, appearing U-shaped in cross section. The

two longitudinal folds are composed of many smaller longitudinal folds.

The retractor muscles of the proboscis consist of three pairs of middorsal, two pairs of lateral, and two pairs of ventral muscles. No protractor muscles could be identified as such (fig.35 ).

The dorsal retractor muscles attach to the medial walls of the middorsal fold. The muscle band which attaches to medial wall of the left fold joins to the muscle band which attaches to the medial wall of the right hand fold so that for each pair of dorsal retractor muscles, only one thick muscle band runs backward obliquely to the dorsal body wall. The dorsal retractors pass thru the septa of the injector organ and attach to the body wall in setigers 2,3, and 4.

The lateral pairs of retractor muscles attach to many of the small folds of the proboscis and converge and pass backward obliquely to the dorsolateral body wall below the lowest band of the dorsolateral longitudinal muscles in setigers 3 and 4.

The ventral retractor muscles extend from the ventral wall of the proboscis to the ventral body wall in setigers 3 and 4.

Muscular Ligaments. Although supporting mesenteries are almost totally lacking and muscular septa are lacking throughout most of the body, there are numerous, thin muscle bands, surrounded by a layer of connective tissue and peritoneum, which hold the alimentary canal in position in the

coelom. They are most numerous in the branchial region where they form a series attaching to the dorsolateral walls of the intestine and a series of ligaments which cross the coelom between the intestine and the ventral body wall (fig.36 ).

Ventrally, a pair of muscular ligaments attach on either side of the ventral blood vessel, run posteriorly, passing on either side of the ventral nerve cord, and connect to the ventral body wall beneath the oblique muscles. They usually span two segments. A similiar pair of ligaments runs anteriorly from the gut wall to the ventral body wall. The two pairs of ligaments cross each other beneath the intestine (fig. 36).

In the segments which contain the large anterior nephridia, a ligament attaches to the medial part of the nephrostome near the ventral blood vessel. The ligament runs forward through two segments and attaches to the gut near the ventral blood vessel. The ligament which attaches to the first nephridium runs to the junction of the stomach and the intestine.

Discussion. The body wall musculature of Ophelia denticulata is the same in many respects as that which has been described by Claparède (1869) in O. radiata, Brown (1938) in O. rathkei (as O. cluthensis), McIntosh (1915) in O. limacina, and Hartmann-Schröder (1958) in O. remanei. Although de Saint-Joseph (1898) stated that O. denticulata (as O. neglecta) does not have a circular muscle layer, well developed bands of circular muscle occur in the prebranchial and postbranchial

regions. The circular muscle layer is not as well developed in the branchial region but it is present as regularly spaced single fibers.

Mush has been written concerning the function of the injector organ. Claparède (1869), de Saint-Joseph (1898), Brown (1938) and Hartmann-Schröder (1958) review the literature concerning it. Claparède called it the injector organ because he believed that it contracted and forced coelomic fluid into the "head". The increased pressure caused the "head" of the worm to become more turgid which aided the worm in its burrowing activities. De Saint-Joseph stated that the injector organ is allied to the esophageal diaphragm of the terebellids.

The muscles associated with the setal sacs in O. denticulata are much the same as described in O. rathkei by Brown (1938) and in other opheliids (Hartmann-Schröder, 1958). The notopodial and neuropodial setal sacs are conical invaginations of the epidermis (Hartmann-Schröder, 1958) which extend a short distance into the coelomic cavity and are covered by a thin layer of peritoneum (fig. 32 ).

## NEPHRIDIA

General. In papers concerned primarily with the taxonomy of species of Ophelia, the number and location of nephridiopores are usually indicated. Between three and six pairs, located in the anterior part of the branchial region, are characteristic of the genus.

Hartmann-Schröder (1958) has studied four species of

Ophelia (O. rathkei, O. remanei, O. radiata, and O. limacina) and found that two types of nephridia are present in O. remanei and O. rathkei. She distinguished true nephridia ("echten Nephridien") from transformed nephridia ("umgewandelten Nephridien"). The true nephridia are located in the anterior part of the branchial region. The transformed nephridia are smaller and are located posterior to the true nephridia. In O. remanei there are three pairs of true nephridia located in setigers 14-16 and additional transformed nephridia in the posterior part of the body. Although Hartmann-Schröder did not find transformed nephridia in the abdominal region of O. radiata, Claparède (1869) indicated that segmental organs exist in all the branchial and postbranchial segments. Although Brown (1938) found only three pairs of nephridia in setigers 12-14 in O. rathkei, Hartmann-Schröder (1958) found additional transformed nephridia in the branchial region of the same species. Schneider (1887), in his description of the species O. denticulata (as O. neglecta), pointed out that there are six pairs of nephridiopores on branchial segments 3-8. De Saint-Joseph (1898), who gave a more detailed description of the same species, indicated in one part of his paper (page 372) that nephridiopores were found on setiger 12 and on each of the following three segments. In the same paper (page 375) he indicates that O. denticulata has six pairs of brown colored segmental organs located in setigers 12-17. De Saint-Joseph did not describe any additional nephridia.

Thus it appears that in all the species of Ophelia

that have been studied, large pairs of true nephridia are present, the number of pairs being constant for a species. Some species of Ophelia have additional pairs of transformed nephridia.

According to Hartmann-Schröder (1958) the nephridia in all the genera in the family Opheliiae are of the metanephridia type except in Euzonus. The species of Euzonus have protonephridia (MacConnaughey and Fox, 1949 and Hartmann-Schröder, 1958).

The specimens of O. denticulata observed in this study have two types of nephridia. The six more anterior pairs open to the outside through nephridiopores which are located slightly anterior to the parapodia of setigers 12-17 inclusive. These are the nephridiopores which were observed by Schneider (1887) and de Saint-Joseph (1898) in their investigations of the same species. The second type of nephridia opens to the outside through nephridiopores located slightly anterior to the parapodia of setigers 18-28. These nephridia are similar, in some respects, to the transformed nephridia described by Hartmann-Schröder (1958) in O. rathkei and O. remanei.

Anterior Nephridia. The nephridiopores of the six pairs of anterior nephridia are located in setigers 12-17. Each nephridium is actually located in two adjacent segments, the nephrostome being open to the perivisceral coelom of the segment anterior to the one in which the nephridiopore is located. The nephridia can be divided into three regions: the nephrostome and ciliated nephrostomial lips; a broad, vertical, funnel-shaped

region; and a horizontal relatively thick walled tubule (fig. 43).

The nephrostome is a wide opening which faces upwards and anteriorly, surrounded by heavily ciliated lips consisting of a higher posterior lip and a lower anterior lip.

The posterior lip attaches to both the dorsal and ventral segmental blood vessels in the area between the oblique muscle layer and the intestine. A short portion of the lip spans the distance between the two blood vessels. The vessels are practically surrounded by the posterior nephrostomial lips, which become an integral part of the wall of the blood vessel.

The anterior lip attaches to the dorsal and ventral segmental blood vessels and runs parallel to the posterior lip.

Below the nephrostomial lips, the wide funnel-shaped region descends ventrally between the oblique muscle bands. A short distance below the oblique muscle layer the funnel narrows and turn posteriorly continuing as the nephridial tubule.

The nephridial tubule has a uniform diameter for most of its length. It extends posteriorly almost as far as the setal sacs of the following segment where it becomes expanded in the region of the nephridiopore. A short mesentery, which is composed of a double layer of peritoneum, connects the tubule to the body wall. A portion of the wall of the tubule folds over, partially blocking the nephridiopore.

The cells lining the nephridium are similar in all regions

of the nephridium except for the cells which surround the nephridiopore. Typically, the cells are short, ciliated columnar cells with finely granular cytoplasm. The centrally located nuclei are round to oval, without a distinct nucleolus, but with scattered dark staining granules. Dark staining fibers or ciliary roots extend from the cilia into the cell and end close to the nucleus. The cells located around the nephridiopore are non-ciliated, tall, narrow, and tightly packed. The nuclei are located toward the distal or free end of the cell. All the regions of the nephridium, except the lips of the nephrostome, are covered externally by a thin layer of peritoneal tissue.

While checking some serial transverse histological sections of a small specimen (32 mm. long x 3 mm. wide), it was noticed that the six anterior pairs of nephridia were reduced in such a way that only the narrow tubule was present. The convoluted nephrostomial lips, the funnel-shaped region, and nephridiopore were absent. The tubule began at the junction of the ventral segmental vessel and the intersegmental vessel and extended posteriorly to the area where it should open to the outside through the nephridiopore. In a somewhat larger and presumably more mature specimen (61 mm long x 5 mm wide), the six anterior pairs of nephridia, although not completely developed, lacked only the large convoluted nephrostomal lips. The six pairs of anterior nephridia were observed, in histogical sections, to be completely developed in a large (100 mm long), sexually mature specimen.

Under certain unnatural conditions (placing the specimen in 8.0% $MgCl_2$) spawning could be induced in sexually mature specimens. Gametes, either eggs or sperm, were extruded through the nephridiopores of the anterior nephridia. In histological sections, gametes and coelomocytes were often seen in the lumen of the nephridia. No leakage of coelomic fluid through the nephridiopores has been observed to occur under natural or unnatural conditions.

Posterior Nephridia. Eleven pairs of nephridia, morphologically different from those described above, are found in setigers 17-28. In these segments, the nephridia occupy the same relative position as do the anterior nephridia. The nephridium spans two adjacent segments. The nephrostome opens in the segment anterior to the one in which the nephridiopore opens.

The nephridia are composed of: a long, ciliated nephrostomial lip attached to the anterior face of the ventral segmental blood vessel; a vertical, descending tube; a small ciliated nephrostome located dorsally where the nephrostomial lip and the descending tube join; and a horizontal, tubule which extends from the base of the descending tube to the nephridiopore (fig. 44 ). Most of the nephridium is located either between or below the oblique muscle bands. As in the anterior nephridia, all the regions of the posterior nephridia are ciliated and all except the nephrostomial lip is covered by a thin layer of peritoneal tissue. Thin peritoneal mesenteries span the short distance between the nephrostomial

lip (and ventral segmental blood vessel) and the descending tube. Another mesentery, which connects to a longitudinal muscle bundle, supports the horizontal tubule along its whole length.

The ventral segmental blood vessel bifurcates not far from its origin at the posterior ventral vessel to form the intersegmental vessel and the afferent branchial vessel. The afferent branchial vessel lies lateral and somewhat posterior to the first half of the intersegmental vessel. The intersegmental vessel curves posteriorly, crossing behind the afferent branchial vessel, and ends blindly near the end of the adjacent segment. The parts of the nephridium follow the course of these two vessels. The nephrostomial lip lies adjacent to the afferent branchial vessel; the descending nephridial tubule and the horizontal nephridial tubule lie adjacent to the intersegmental vessel. None of the nephridial tissue joins to the dorsal segmental vessel.

In contrast to the anterior nephridia, the nephrostomial lips of the posterior nephridia do not become filled with blood nor are they folded in the same manner. The lip, which is attached to the anterior side of the afferent branchial vessel, curves upward to form a shallow, V-shaped ciliated groove (fig. 44 ). The groove connects to the posterior side of the nephrostome and continues along the afferent branchial vessel to the body wall. The membrane connecting the nephrostomial lip (and blood vessel) to the descending nephridial tubule probably holds the nephrostome in the proper position

relative to the rest of the nephridia. It may also act as a barrier or baffle which deflects coelomic fluid toward the nephrostomial lip.

The descending nephridial tubule lies medial to the nephrostomial lip. It descends between the oblique muscle bands into the ventrolateral coelom. The tubule is narrower at the top than it is at its base and it is elliptical in cross section. A thin suspensory peritoneal membrane connects the medial side of the tubule to the ventral body wall. The nephrostome opens into the dorsal part of the descending nephridial tubule and the horizontal nephridial tubule leaves at right angles from the base of the descending tube.

The diameter of the horizontal nephridial tubule remains unchanged up to the nephridiopore. Near the nephridiopore, the horizontal nephridial tubule enlarges, bulb like, and then constricts forming either one or two small nephridiopores. The lumen of the horizontal nephridial tubule is so narrow that the tips of the cilia touch in the center.

The structure of the cells is similar in each of the regions of a posterior nephridium, consisting of tall, ciliated columnar cells having thick limiting membranes. The coarsely granular nuclei, which are located near the ciliated end of the cell, are irregularly shaped and have a large nucleolus. Extensions of the cilia extend to the nucleus. The cells of the horizontal tubule are nearly cuboidal. The cells of the distal expanded part of the horizontal tubule are narrow, closely-packed, non-ciliated and covered by a thin layer of

cuticle. The nuclei are round to oval and contain large granules.

Brown granules (excretory products?) are found in the cytoplasm of the cells of the posterior nephridia except in the cells surrounding the nephridiopores and in the expanded portion of the horizontal tubule near the nephridiopore. The brown granules are evenly and densely distributed in the cells of the descending nephridial tube. In the nephrostomial lips and horizontal tubule the granules are concentrated near the ciliated end of the cell. The cytoplasm of the basal part of the cells is clear and non-granular.

Serial histological sections show that the posterior nephridia are as well developed in the smaller specimens (32 mm. long) as in the large specimens (100 mm. long). Although sperm are occasionally seen in the lumen of the posterior nephridia, the emission of gametes through the nephridiopores of the posterior nephridia has never been observed even though observations were made while the specimens were spawning through the nephridiopores of the anterior nephridia. However, leakage of coelomic fluid through the posterior nephridiopores has been observed in specimens placed in unnatural conditions.

Discussion. No detailed description of the anterior nephridia has been found for any species of Ophelia. De Saint-Joseph (1898), who did not report the presence of any posterior nephridia, observed brown granules in the cells of the segmental organs of O. denticulata (as O. neglecta). I have not been able to find brown granules in the anterior nephridia of

O. denticulata.

The "transformed" nephridia that Hartmann-Schröder (1958) found in O. remanei and O. rathkei, although found in the same relative location, are morphologically different from the posterior nephridia found in O. denticulata. In O. remanei, the nephrostome, which is larger than that of the "true nephridia", does not extend into the preceding segment. The nephrostome is also large and funnel-like. As mentioned above, the nephridia in O. denticulata span two segments, the nephrostome is not funnel-like, and the nephrostome is smaller than that of the anterior (true) nephridia. In O. rathkei, although the"transformed" nephridia span two segments, the nephridial tubule is composed of one main tube and many smaller tubules. Hartmann-Schröder (1958) states that the transformed nephridia possibly do not open to the outside. In O. denticulata the nephridial tubule is single and empties through one or two nephridiopores.

Although Hartmann-Schröder (1958) has stated that all the opheliids, except those in the genus Euzonus, posses metanephridia, she was not justified in doing so since the function and embryological development as well as the anatomy of the segmental organ must be known before one can be certain of the type of nephridium. This is especially true when one is trying to decide whether or not the segmental organ in question is a metanephridium, a metanephromixium, a mixonephridium, or a coelomoduct.

There are two morphologically different types of

nephridia found in O. denticulata. Do both types of nephridia have the same function, or are they also different functionally? Since no embrylogical or physiological evidence is available it is impossible to be sure of the function and hence the type of nephridia found in O. denticulata.

However, since both types of nephridia are open to the coelom and solenocytes are absent, the protonephridial type can be ruled out. Emission of gametes through the nephridiopores of the anterior nephridia suggests a genital function. If the excretory function is lacking in the anterior nephridia and if embryological evidence shows a mesodermal origin, then the anterior nephridia are actually coelomoducts. If they are not of mesodermal origin but still serve as an exit for gametes, then the anterior nephridia are mixonephridia, modified as in some sedentary polychates (eg., serpulids and terebellids) for genital discharge only. Usually it is the posterior nephridia which are modified for genital discharge and the anterior nephridia are specialized for excretion in terebellids and serpulids (Borradaile, et al.).

In O. denticulata, the posterior nephridia contain brown granules in the cytoplasm of the cells. Emission of gametes from the nephridiopore of the posterior nephridia has not been observed (see above). This suggests that the posterior nephridia, which posses a nephrostome, are specialized for excretion only. If so, the posterior nephridia would be classified as metanephridia.

## INTEGUMENT

Cuticle. The entire body surface of O. denticulata is covered by a cuticle composed of superimposed fibrous layers. The outermost layers contain striations which cross at right angles causing the iridescence characteristic of O. denticulata and other species of Ophelia.

The mouth, pharynx (proboscis), rectum, and nephridiopores are lined with a thin layer of cuticle. The cuticle varies in thickness in different body regions. The cuticular covering of the palpode is thinner than the underlying epidermis. The numerous annuli of the prebranchial region are made visible externally by regular thickened ridges of cuticle (fig. 39). In a specimen 100 mm. long, the cuticular ridges are 85 micra thick. In the areas between the ridges, the cuticle is between 25 and 30 micra thick. The body wall of the branchial and postbranchial regions of the same specimen is not annulated and the cuticular layer is of a uniform thickness, measuring 40-45 micra thick. The cuticular covering of the anal papillae is thinner than that covering the postbranchial segments.

Epidermis. The epidermal layer lying beneath the cuticle is composed of supporting cells, gland cells, and other specialized cells. The thickness of the epidermis varies depending upon the presence of annuli, the body region, and the number of gland cells present.

Where there are no glands, the supporting cells are columnar with blue staining (Hematoxylin-Eosin) basally to

centrally located nuclei. When numerous glands are present, the supporting cells, which fill the areas between the glands, become packed and compressed (fig.45). The distal part of the cells contains the nucleus and most of the cytoplasm. The basal part of the cells is composed of elongated cell membranes which fuse together forming sheets of membranous tissue between and beneath the basal part of the glands. The cytoplasm of the supporting cells is granular. The oblong nuclei contain small, blue staining granules and do not have distinct nucleoli.

Three types of gland cells were distinguished in the epidermis, based on the staining reaction of the secretory product to Hematoxylin-Eosin and on the morphological appearance of the cells. The three types of gland cells have been arbitrarily designated types A, B, and C.

The gland cells seldom occur singly but are usually found in flattened spherical packets which share a single, common pore (fig. 49). Various combinations of cells compose a gland packet, such as: type A cells only; type B cells only; type C cells only; type B and C cells; or type A and B cells. When combinations of gland cells occur, type B gland cells are always found in the center, and type C cells on the periphery of the packet. Type A gland cells are also found on the periphery of the packet but one type A cell may occur in the center of the packet. When all three types of gland cells occur in the same packet, type B cells are in the center, type C cells surround the type B cells, and the type A cells are located between adjacent type C cells. The distal ends of all

the gland cells in a packet converge and empty to the outside through one pore (fig. 49 ).

The narrow, elongate type A gland cells usually become coiled basally (fig. 46 ). The cytoplasm is packed with secretory products such that the nuclei are not visible. The secretory products are closely packed ropy strands which stain dark blue with Hematoxylin-Eosin and have a strong positive reaction to Safranin-O, and Thionin. Type A cells have a weak positive reaction to P.A.S.

Glandular cells designated type B are also elongate, coiled basally, and straight near the pore (fig.46 ). The nuclei, which are nearly as wide as the cell, contain granules staining blue with Hematoxylin-Eosin. Type B gland cells are filled with spherical granules which do not stain with Hematoxylin-Eosin, Safranin-O, or Thinonin. These granules give a weak positive reaction to P.A.S. and also stain light blue to green with Gomori's trichrome stain.

Type C gland cells are also elongate, but do not coil basally. The nucleus is small in comparison to the width of the cell, stains intensely blue with Hematoxylin-Eosin, and is located on the periphery of the cell. Type C gland cells are filled with a homogeneous secretory product which stains a light blue with Hematoxylin and stains light blue with Thionin.

Generally, dense accumulations of gland packets occur in the epidermal layer of the middorsal body wall and along the lateral and ventrolateral body wall in line with the parapodia in all body regions. They occur, but not as densely,

on the dorsolateral and ventral body wall and in the midventral groove. In addition, various regions of the body can be characterized by the presence of a particular combination of gland cells.

Prebranchial Region. This region is generally well supplied with epidermal gland cells. The entire region, with the exception of the palpode, is deeply annulated causing the epidermal layer to become constricted beneath the thickened cuticular ridges (fig. 39 ). The packets of gland cells are located between the constrictions. Narrow, columnar supporting cells occur in the constricted portion of the epidermis. Extensions of the cuticle project into and sometimes through the constricted part of the epidermis (fig. 51 ).

The most widespread type of gland cell packet is composed solely of type B gland cells, except for an occasional type A or type C gland cell. The number of type A gland cells, included with the type B gland cells, increases toward the dorsal midline. Type A gland cells, which are most numerous in the dorsal midline, progressively increase in number in each succeeding prebranchial segment. Packets of type C gland cells are most numerous in the zone slightly anterior to the notopodial setal sac. In each succeeding setiger, the zone of type C gland cells enlarges dorsoventrally. At the end of setiger 9 the gland cell packet of type C cells is so large and numerous that a prominent glandular ridge is formed above the notopodial setal sac (fig. 31 ). Packets of type A gland cells are found on the posterior part of the glandular ridge

near the notopodium.

The prostomial palpode contains only a few, scattered type A gland cells. Most of the epidermis of the palpode is composed of short columnar cells with centrally located nuclei.

Branchial Region. As in the prebranchial region, the dorsolateral body wall, lateral groove, and the lateral part of the ventrolateral ridges of the branchial region contain numerous epidermal gland cell packets composed primarily of type B gland cells, which occasionally contain type A or C gland cells. Since the branchial region has no annuli, the thickness of the epidermal layer is more uniform. However, the dorsal epidermal layer is thicker than the ventral. In the dorsal part of the lateral groove, where the oblique muscles attach, the epidermal layer is thinner than that of the dorsal body wall.

The middorsal epidermis is composed almost solely of numerous gland cells of type A. They are also numerous in the area immediately anterior to the parapodia.

The zone of type C gland cell packets which were well developed near the notopodia of the posterior prebranchial setigers, become progressively reduced in the first four branchial setigers and are absent in branchial segment 5. Throughout the rest of the branchial region, type C gland cells may be occasionally found in packets composed primarily of another type of gland cell.

A continuous row of packets of gland cells in line with the notopodial setal sacs, extends the entire length of

the branchial region. They are composed entirely of type B gland cells and project below the level of the epidermis and are surrounded by a layer of peritoneum.

The epidermis of the branchiae contains relatively few gland cells, which occur singly, not in packets. A few scattered gland cells of type A occur singly in the enlarged base of the gill. Gland cells of type B, although not numerous, can also be found singly in the branchial epidermis.

The branchiae, which can extend and contract longitudinally, become highly folded when contracted. Also, the epidermis contains deep grooves running at right angles to the long axis of the gill. The branchial capillaries, which connect the afferent and efferent branchial vessels, are located in these grooves (figs. 27 and 28).

The epidermis is composed of two types of cells, ciliated and nonciliated. The ciliated cells are distributed over the entire surface of the branchiae but not in the enlarged base of the gill. Since cell membranes are not clearly visible, individual supporting cells can not be distinguished. However, the nuclei of adjacent cells which are located in the distal portion of the cell nearly touch each other. The membranes of the basal part of the cells are drawn out and fibrous appearing. Although the exact limits of the ciliated cells have not been seen, distinct basal granules, ciliary roots, and nuclei are visible. In sections stained with Hematoxylin-Eosin, a single, large, blue staining nucleus with a distinct nucleolus is found in the basal part of the ciliated cell. The

ciliary roots extend from the basal granules to the nucleus. In the non-ciliated supporting cells, the nuclei are smaller, and more granular than those of the ciliated cells, and a nucleolus is absent. The long axis of the nucleus is parallel to the long axis of the cell.

Postbranchial Region. The distribution of glands in the postbranchial region is similar to that of the branchial region, although there is a general tendency toward a reduction in the number of packets of gland cells. They are mostly composed of gland cells of type B with occasional cells of type A or type C. Although gland cells of type A are most numerous in the dorsal midline they are not as numerous as in the branchial region and are lacking in postbranchial segments 4 and 5. As in the branchial region, concentrations of gland cells of type A occur immediately anterior to the postbranchial parapodia.

Gland cells of type C are not abundant in the postbranchial region. Some occur with gland cells of type A and B in the middorsal part of the posterior end of postbranchial setiger 1.

Anal Papillae. The anal papillae contain scattered packets of cells composed of both types A and B. The supporting cells are nonciliated, columnar, containing large oval nuclei.

Specialized Epidermal Cells. Specialized epidermal cells or groups of cells are present. The "branchial fenestrations" (Tebble, 1953), lateral organs (de Saint-Joseph, 1898) and nuchal organs (Hullier, 1951) have been reported by the

above authors as being present in O. denticulata. The setal sacs, also epidermal structures, have been described above (see musculature).

Branchial fenestrations, named by Tebble (1953), occur as vertical rows of regularly spaced tubular pores in the lateral grooves and in the midventral groove of the branchial region and in the first postbranchial segment. In cross sections, the pore passing through the cuticle is funnel shaped, the wide end occuring at the external surface of the cuticle (fig. 54). Basal granules line the rim of the funnel and numerous cilia extend to the outside from the basal granules. Numerous ciliary roots extend inward from the basal granules into the epidermal layer. The ciliary roots fan out beneath the cuticle and end near 4-5 large, oval nuclei. Each of the nuclei contains fine, blue staining granules and a distinct nucleolus. None of the nuclei appear to be associated with a separate, distinct cell. Instead, all the nuclei and their associated ciliary roots appear to be surrounded by a single enclosing membrane. In sections stained with Hematoxylin-Eosin, the cilia and ciliary roots stain red and the nuclei stain blue. A homogeneous, red staining secretion occurs in many of the pores.

Packets of specialized epidermal cells occur in the epidermis of the palpode and are also found irregularly distributed in other regions of the body. Fibrous processes extend into but not through the cuticle from the cell packet causing a slight bulge in the cuticle. Although as many as

four nuclei have been seen in the cell packet, no individual cells could be distinguished.

The lateral organs are located between the notopodial and neuropodial setal sacs in each setigerous segment (fig. 52). In all the setigerous segments, except setiger 1 and setigers 29 through 32, a small dark spot is found on the neuropodial postsetal lobe. A lobe of the lateral organ ganglion enters the neuropodial postsetal lobe. This is the location of a group of ciliated cells containing dark blue staining nuclei and ciliary roots. The cilia pass to the outside through a thin layer of cuticle. The lateral organ is composed of a large ganglion which is directly innervated by a nerve branching off the ventral nerve cord. A narrow papilla, containing nerve tissue and ciliated cells, extends from the ganglion to the exterior (fig. 53 ). It is the papilla which can be seen on the external surface between the parapodial lobes. Retractor muscle fibers pass into the center of the papilla from the setal sac.

Discussion. A brief discussion of the cuticle of O. denticulata (as O. neglecta) was given by de Saint-Joseph (1898). The cuticle of O. denticulata is the same as that which has been described in O. rathkei (as O. cluthensis) by Brown (1938) and in O. limacina by Hartmann-Schröder (1958). In this study, observations made on the cuticle only tend to confirm that which has been written by other investigators.

The only published description of the epidermis of Ophelia is that given by Hartmann-Schröder (1958), who

described the epidermis of O. limacina. She stated that the epidermis is similar in all opheliids. In O. limacina, clear, round gland cells with irregularly formed nuclei and a dark blue fibrous substance is found in close proximity to the clear gland cells. O. remanei posseses no epidermal glands. In other opheliids, dark blue mucus glands lie among the epidermal cells.

The functions of the three types of gland cells found in the epidermis of O. denticulata are not known. However, living specimens exude copious amounts of mucus along the dorsal midline and also from the areas immediately anterior to the parapodia of the branchial and postbranchial regions. The continuous sheet of mucus secreted from the dorsal midline may extend as much as 2 cm. from the body wall. Since the greatest concentration of gland cells of type A occurs in the epidermis of the dorsal midline, and immediately anterior to the parapodia, these cells are evidently producers of mucus.

The nuchal organs of the specimens observed in this study are structurally the same as those described by Rullier (1951).

Hartmann-Schröder (1958) pointed out that Lang (1894) believes that lateral organs are homologous to the dorsal cirri of the neuropodium and thus function as tactile organs. The scattered groups of cells which send fibrous processes into the cuticle (see above) may also be tactile organs.

The structure and function of the "branchial fenestrations" has not been reported. Organs containing nonmotile cilia

usually have a sensory function (Borror, personal communication). Also, cilia which lack the pair of axial filaments are non-motile. Therefore, electron micrographs of these ciliated organs could aid in determining their function.

## ALIMENTARY TRACT

General. The alimentary tract of Ophelia denticulata is a straight tube which can be divided into five morphological regions: mouth, pharynx esophagus, stomach, intestine, and rectum. Although the gut is not convoluted, some regions contain numerous longitudinal folds. In actively feeding individuals, all regions of the gut are packed with sand grains. McConnaughey and Fox (1949), who studied Euzonus (Thoracophelia) mucronata, believe that the worm derives its nutrition from the organic matter adsorbed to sand grains and from protozoa, bacteria, and other small organisms adhering to the sand or otherwise associated with it. Septa are found only around the pharynx (see injector organ) and in the last five setigerous segments around the rectum. Contrary to the opinion of de Saint-Joseph (1898), the intestine is not constricted or held in place by septa. However, muscular suspensory ligaments, especially numerous in the branchial region, hold the gut in position in the coelomic cavity. A voluminous blood sinus occurs in all regions, except the pharynx, between the gut epithelium and the peritoneal muscle coat of the outer gut wall.

The peritoneal covering of the intestine, and to a

lesser extent that of the stomach and the esophagus, becomes greatly thickened and contains numerous yellowish-brown granules (fig. 69 ). This modified peritoneal layer has been identified as chloragogen tissue by Schaeppi (1894). In dissected specimens, the outer surface of the intestine is colored dark brown and has a spongy texture.

Mouth and pharynx. The mouth is a ventral transverse slit located at the posterior margin of setiger one. A short buccal cavity leads directly from the mouth to the highly folded, eversible pharynx. The buccal cavity is lined with nonciliated, columnar cells. The thin cuticular lining of the buccal cavity and that of the anterior part of the pharynx has a fine striated or textured appearance. The inverted pharynx extends from setiger one, slightly anterior to the mouth, to the anterior end of setiger four. The posterior part of the pharynx is enclosed within the anterior conical septum of the injector organ (fig. 35). The middorsal wall of the pharynx is folded downward almost to the ventral wall, dividing the pharynx into two longitudinal halves (fig.57). Each half is further subdivided by numerous, smaller longitudinal folds. The folded pharynx nearly fills the coelomic cavity. When everted by the pressure of the coelomic fluid, the pharynx becomes a smooth walled, bilobed sac which is a bright red color. The anterior lobe is formed by the eversion of the dorsal and anterior part of the pharynx and the posterior lobe by the eversion of the ventral part located posterior to the mouth.(fig.35 ). The slitlike opening between the two lobes

of the everted pharynx leads to the esophagus. In living specimens the ciliated surface of the everted pharynx has a shimmering appearance resulting from the waves of ciliary movement which pass over the surface. A continuous flow of water around the pharynx is maintained by the action of the cilia. Although the everted pharynx is colored bright red, no blood sinuses associated with the pharyngeal wall have been detected in histological sections. A series of thick muscle fibers retract the pharynx (see musculature).

The pharyngeal epithelium is composed of tall ciliated columnar cells, closely packed together. They are narrow basally and flare out at the free (distal) end. The nuclei are elongate, granular, and stain dark blue with Hematoxylin-Eosin. Ciliary roots extend from the distal end of the cells to the basally located nuclei. The cytoplasm is filled with fine, red staining granules (Gomori's stain).

Narrow, elongate gland cells, containing a granular secretion, occur rarely in the pharyngeal epithelium. The secretory product gives a positive reaction to the P.A.S. technique. Small granules, staining metachromatically with Thionin and Safranin-O, are scattered throughout the pharyngeal epithelium. The circular, longitudinal, and diagonal muscle layers lie closely appressed to the pharyngeal epithelium.

Esophagus. The transition from pharynx to esophagus occurs near the point where the pharynx passes through the outer conical septum of the injector organ (anterior end of setiger 4). When the pharynx is everted, the esophagus is

shifted slightly forward. A thin layer of circular muscle fibers, derived from the injector organ, covers the anterior part of the esophagus. The wall of the esophagus, in which a blood sinus is enclosed, exhibits various degrees of folding. Occasionally the esophagus may have a deep middorsal fold or many, smaller longitudinal folds. In other instances, only minor "wrinkles" occur in the esophageal wall. The diameter of the esophagus is less than that of both the pharynx and the stomach.

The transition of cell types at the junction of the pharynx and the esophagus is gradual. The esophageal epitheium is composed of ciliated columnar cells with rounded nuclei which are nearly as wide as the cells (fig. 59). Ciliary roots extend into the cytoplasm, ending near the nucleus. The cytoplasm is granular distally and clear basally. Although no gland cells have been found, small granules, similar to those found in the pharyngeal epithelium, are scattered among the cells. The granules give a positive reaction to P.A.S., Thionin, and Safranin-O.

Stomach. The junction between the esophagus and the stomach, marked by an increase in diameter and longitudinal folding of the ventral and ventrolateral wall, occurs between setigers 5 and 6. The midventral fold, the origin of the gastric typhlosole, begins at the anterior end of the stomach. The medial branch of the ventral blood vessel is enclosed by the typhlosole. Posteriorly, the typhlosole enlarges in height and subdivides into additional longitudinal folds (fig.18 ).

Also, two pairs of ventrolateral folds appear, one pair on each side of the typhlosole. Toward the middle of the stomach, the lumen is nearly filled by the folds of the typhlosole (fig. 19 ). At the posterior end of the stomach (setiger 9), the ventrolateral folds become greatly reduced. The gastric typhlosole, at this point, consists of a double-walled vertical "peduncle" which expands at the top forming two, horizontal, blind pouches (gastric caecae). The pouches separate from the "peduncle" and extend into the anterior end of the intestine.

The epithelial cells of the anterior part of the stomach are structurally the same as those of the esophagus. However, in sagittal sections, the ciliated epithelial cells are not as narrow basally. A layer of tissue, which is histologically similiar to that of the heart body, occurs in the anterior part of the typhlosole. Most of the cells become filled with fine brown granules as the wall becomes more folded (fig. 60 ). Gland cells, regularly interspersed between the ciliated cells, appear in the posterior end of the stomach (setiger 9) and in the typhlosolar epithelium (fig. 61 ). As the goblet-shaped gland cells become more numerous, the basal parts of the ciliated cells becomes narrower. The distal ends are covered by a layer of short, bristle-like filaments (brush border, striated border) between which the cilia pass. A tangential section shows the small pores of the gland cells as being located where 3 or 4 adjacent ciliated cells meet. The gland cells and ciliated cells of the typhlosole are more elongate than those of the dorsal and lateral parts of the gastric

epithelium. The nuclei of the gland cells are located in the wide basal parts of the cells. The secretory products are homogeneous in the basal parts of the cells and coarsely granular in the distal parts of the cells. The homogeneous portion of the secretory product stains intensely with Ehrlich's hematoxylin, Thionin, and Safranin-O. The granular secretory product does not stain with Safrain-O, P.A.S., or Thionin but stains red with eosin and intensely red with Gomori's trichrome stain.

Intestine. At the anterior end of setiger 10, a constriction marks the transition from the stomach to the intestine. From this point, the intestine, which does not become coiled or change in diameter, extends to the end of the branchial region. Although the posterior end of the gastric pouch becomes separated from the floor of the intestine in setiger 10, the gastric pouch extends posteriorly as far as setiger 12. Beneath the gastric pouch, in setiger 11, the intestinal typhlosole originates as a shallow infolding of the intestinal epithelium. The anterior part of the typhlosole is filled with connective tissue. Near the end of setiger 12, the connective tissue recedes on the left side of the typhlosole and the intestinal sinus extends into the typhlosolar lumen (fig. 23 ). On the right side, near the base of the typhlosole, the epithelium becomes heavily ciliated and forms a groove which extends the length of the intestine (fig. 68 ). As the ventral typhlosole increases in height and width, as increasing amount of chloragogen tissue is found within the typhlosolar

lumen.

On a histological basis, the intestine is divisible into three regions. The change from one region to another begins in the typhlosolar epithelium and then continues to the lateral and dorsal walls of the gut. In the first region, although there is a distinct morphological dividing line between the stomach and the intestine, the posterior part of the stomach and the anterior part of the intestine are composed of the same types of cells (fig. 62 ). The large, granular gland cells first disappear in the intestinal typhlosole in setiger 11. In the region of setiger 15, the granular gland cells are no longer present in the intestinal epithelium.

In the second region, setiger 15 to setiger 25, the intestinal epithelium is composed of ciliated columnar cells which contain a centrally or basally located nucleus. Dense concentrations of fine, brown granules are located in the cytoplasm of the distal part of the cells. The free ends of the cells, in addition to being ciliated, have a brush border. There are no ciliary roots visible in these cells. The brush border of the cells gives a strong positive reaction to P.A.S. but does not stain with Safranin-O or Thionin. Individual gland cells containing a finely granular secretory product are found scattered among the ciliated cells. The glandular cells, being narrow at both ends, are a modified goblet-shape (fig 63). The gland cell contents are lightly stained with Hematoxylin, Thionin, and Safranin-O.

The third region,extending from setiger 25 to setiger 27,

is recongnized by the presence of ciliated columnar cells in which the distal ends are vacuolated and the brown granules are absent. The vacuoles remain unstained.

Rectum. The transition from intestine to the rectum occurs at the posterior end of the branchial region (setiger 27). The thick peritoneal covering (chloragogen tissue) is not found posterior to the membrane which attaches the dorsal segmental vessel of the last branchial segment (setiger 27) to the outer gut wall (fig. 42 ). The postbranchial segments are bounded by septa which also cover the outer wall of the rectum. A very thin peritoneal membrane and a layer of circular muscle fibers lie outside of the relatively thick septum. Within the rectum, the ventral typhlosole gradually changes over to the anal valve. The blood sinus of the wall of the rectum ends at the posterior end of setiger 32. The typhlosolar sinus extends into the papillae of the anal valve. The epithelial cells are heavily ciliated, columnar, with a rounded, centrally located nucleus containing a distinct nucleolus. The cilia are more numerous than in the intestine giving a tufted appearance to the rectal epithelial cells. Vacuoles, as seen in the posterior part of the intestine, are lacking. The anal valve, an extension of the ventral typhlosole, is formed at the posterior end of the postbranchial segment 2 (setiger 29). The papillae of the anal valve are composed of non-ciliated columnar cells. The rectal epithelium has a thin cuticular lining, the brush border being absent. No gland cells have been found.

Three ciliated organs extend the length of the rectum (setiger 28-32) (fig. 24 ). One is located on the left side of the anal valve; the other two are located dorsolaterally in the rectal wall. The ciliated organs are composed of tall, heavily ciliated columnar cells with numerous ciliary roots extending from the surface of the cell to the level of the nucleus (fig. 66 ). The oval nuclei of adjacent cells are all located centrally on the same level.

Discussion. The publications of Schaeppi (1894) and Hartmann-Schröder (1958) give the most detailed information on the alimentary canal of the species of Ophelia. Brown (1938), Claparède (1869) and de Saint-Joseph (1898) describe the gross anatomy of the alimentary canal of O. rathkei (as O. cluthenses), O. radiata, and O. denticulata (as O. neglecta) respectively but do not give histological details.

From the available descriptions, it appears that the morphology of the alimentary canal is much the same in all the species of Ophelia that have been studied. However, some apparent morphological differences do occur between the specimens of O. denticulata observed in this study and those species described by the above mentioned investigators. Rectal ciliated organs have not been reported in any of the species of Ophelia. The rectum of O. denticulata is located in the last 5 setigerous segments. Hartmann-Schröder (1958) states that the hind gut of the Ophelia-group begins in the last setigerous segment. De Saint-Joseph (1898) reported that the intestine of O. denticulata (as O. neglecta) is constricted by septa in each segment.

This has not been found to be true in the specimens observed in this study.

Concerning the composition of the gut wall, Claparède (1869) states that the sinus is situated between the two muscle layers of the gut. Schaeppi (1894) found a layer of circular muscle fibers on the outer sinus wall. However, he did not observe either longitudinal or circular muscles on the gut epithelium of O. radiata. Schaeppi (1894) believes that the sinus blood is in direct contact with the gut epithelium because he has not been able to find a limiting membrane between sinus and the gut epithelium. In the specimens of O. denticulata observed in this study, the outer gut sinus wall is composed of the following layers: outer peritoneal layer, muscle fibers (circular, longitudinal, or diagonal), basement membrane, endothelium. The cells of the endothelial layer have long processes which occasionally span the sinus cavity and join to the endothelial layer of the inner wall. The inner gut wall is composed of: an endothelial layer, a basement membrane, and the gut epithelium. A muscle layer has not been found in the inner gut wall. The layers of the gut wall are most easily observed in the posterior part of the intestine (setigers 20-27).

Although Hartmann-Schröder (1958) reported the histological structure of the alimentary canal of various genera of the Opheliidae, she made few statements that applied specifically to the species of Ophelia. She found clear, round gland cells in the pharngeal and esophageal epithelium of O. rathkei and in

the gastric epithelium of the Ophelia-group . No gland cells of this description have been found in the gut epithelium of O. denticulata.

Gland cells containing large granules, such as those found in the posterior part of the stomach and anterior part of the intestine in O. denticulata, were not present in those species of Ophelia studied by Hartmann-Schröder.

Schaeppi (1894) found chloragogen tissue and granules in the intestinal typhlosole of O. radiata. Smaller granules were located in the epithelium of all gut regions except the pharynx. These granules, which are usually concentrated near the distal (free) end of the cells, resemble chloragogen granules but do not fuse to form larger granules. In O. denticulata, fine brown granules are found in the distal parts of the ciliated epithelial cells of parts of the stomach and the intestine. These granules may be the same as those found in O. radiata by Schaeppi.

## NERVOUS SYSTEM

General. The nervous system of Ophelia denticulata is composed of a cerebral ganglion (brain), a pair of circumpharyngeal connectives, a subpharyngeal ganglion and a ventral nerve cord.

The brain is located partially in the small conical palpode and partially in the annulated preoral region (fig.79 ). The circumpharyngeal connectives leave the posterior ventral corners of the brain, roughly follow the course of the ventral

preoral grooves up to the mouth, and then diverge and pass to either side of the mouth opening where they reunite behind the mouth in the space between the two septa of the injector organ, near the end of the third setigerous segment. The subpharyngeal ganglion, the first ganglion of the ventral nerve cord, is formed where the two circumpharyngeal connectives meet. The ventral nerve cord extends as far as the last setigerous segment where it bifurcates sending a major branch into each of the two ventral anal papillae. Along its course, the ventral nerve cord gives off five pairs of nerve branches in each of the setigerous segments.

Brain. The brain, in sagittal section, is elliptical with the long axis of the ellipse tilted posteriorly about 30 degrees (fig. 79 ). In cross section, the anterior part of the brain is also elliptical with the short axis in the dorsoventral plane. Further posteriorly, near the point where the circumpharyngeal connectives are given off, the cross section of the brain is trapezoidal in outline. The brain of a specimen of 45 mm. in length measures, near the origin of the circumpharyngeal connectives, 220 micra dorso-ventrally and 330 micra in the lateral dimension. The midsagittal length of the brain, in a slightly larger specimen (54mm. long) is 180 micra, thus, the brain is wider than it is long and taller posteriorly than it is anteriorly. The brain, although not bilobed, is bilateral.

Two large palpode nerves or processes of the brain, referred to as frontal horns by Schneider (1887), extend from each side of the anterior ventral margin of the brain into the

tip of the palpode. The peritoneal covering of the palpode nerves extends to the lateral walls of the palpode forming a supporting mesentery. The palpode nerves do not give off any branches along their course.

The circumpharyngeal connectives originate on each side of the posterior ventral end of the brain. In addition, two large branches, referred to as occipital horns by Schneider (1887), are derived from the dorsal posterior corners of the brain, and are reflexed anteriorly over the brain. Their origin is dorsal and slightly posterior to that of the circumpharyngeal connectives. Each of the occipital horns forms a broad flattened lobe which lies above the surface of the brain (fig. 74 ) Directly above their point of origin, the occipital horns come into contact with the epidermis. At this point, a small pore passes through the epidermis and cuticle and connects the occipital horns to the outside environment. The pore is located in the shallow groove formed at the junction of the palpode and the annulated preoral region.

The nerves of the nuchal organ originate on the same level but slightly ventral to the origin of the occipital horns. Each nerve extends from the brain to the center of the nuchal organ where it connects to a ganglion. Another pair of nerves, referred to as gangliiform nerves by Schneider (1887), leave the posterior part of the brain from points located laterally between the origin of the circumpharyngeal connectives and the origin of the nerves of the nuchal organ. Each of these nerves, which are smaller in diameter than the nuchal organ nerves, extends

from the brain to the ventrolateral body wall.

The pair of palpode nerves or frontal horns is composed of a central core of nerve fibers surrounded by cells containing oblong nuclei filled with large coarse granules. Numerous large, round blue staining (trichrome stain) nerve cells with large, clear, rounded nuclei occur scattered in the nerves. The nerves are covered by a peritoneal layer, the basement membrane of which forms a relatively thick covering. Near the brain, the nerves contain some vacuolated cells in which the nuclei are displaced to one side of the cell. The brain proper is also covered by a layer of peritoneum. The anterior portion of the brain contains a dorsally located group of vacuolated cells below which occur some rounded blue-staining nerve cells. More posteriorly, a large central mass of nerve fibers is surrounded dorsally and laterally by vacuolated cells and blue-staining nerve cells (fig. 78 ). The large central fibrous mass is composed of the fibers which give rise to the neuropiles (or fibers tracts) of the circumpharyngeal connectives, the nerves of the nuchal organs, the occipital horns, and the small pair of gangliiform nerves. Three bow-shaped superimposed commissures appear toward the posterior end of the brain. Only two of the commissures appear in the same plane (fig. 75 ). The two dorsal commissures, in which the arms of the bow are pointed upward, connect with the occipital horns and the nuchal organ nerves respectively. The ventral commissure, in which the arms of the bow are pointed downward, continues as the circumpharyngeal connectives.

The occipital horns are composed almost entirely of vacuolated cells in which the nuclei are displaced to one side of the cell by the vacuoles. In addition, large vesicles, each of which contains a large, globular secretion, lie adjacent to each other along the length of the occipital horn (fig. 71 ). It has not been determined whether or not the vesicles are interconnected. Also, no connection between the vesicles and the pore which leads to the outside (see above) has been found. The secretion within the vesicles stains dark red with P.A.S. and blue with Thionin.

The eyes, which are simple cuplike clusters of brown granules, are embedded within the brain. There are three eye spots, two located ventrolaterally in the anterior part of the brain, and a third located in line with and posterior to the left hand member of the anterior pair of eyes. No eye spot is found on the posterior right side.

Circumpharyngeal connectives. In their course from the brain to the subpharyngeal ganglion, the circumpharyngeal connectives each give off four major nerve branches. The first two pairs originate from the connectives in the preoral region slightly anterior to the mouth. Although their destination is not precisely known, these nerves extend to the midventral body wall in the region of the anterior lip. The third and largest pair of nerves, similiar in diameter to the circumpharyngeal connectives, originate from the medial sides of the connectives, lateral to the mouth, and extand to the lateral pharyngeal wall,

serving as the stomatogastric nerves. The fourth pair of nerves originate from the connectives in the posterior part of setiger 2 and run forward and laterally, between the epidermis and the body wall muscles, to the setal sacs of setiger one.

Subpharyngeal Ganglion. The subpharyngeal ganglion is situated in setiger three. Immediately posterior to the point where the circumpharyngeal connectives join to the subpharyngeal ganglion, a pair of nerves leave the ganglion and extend to the setal sacs of setiger 2.

A concentration of large blue-staining nerve cells occurs on the medial and ventral sides of the anterior part of the subpharyngeal ganglion. More posteriorly, a lateral commissure forms between the two longitudinal fiber tracts of the subpharyngeal ganglion. Although some nerve cells are located dorsally, the greatest concentration of nerve cells occurs in the ventral and ventrolateral regions of both the subpharyngeal ganglion and the ventral nerve cord.

Ventral Nerve Cord. The ventral nerve cord is structurally the same as the subpharyngeal ganglion. In each setigerous segment, the ventral nerve cord gives rise to five pairs of lateral nerves. The last, or fifth, pair (pedal nerves) runs laterally, between the epidermis and the body wall musculature to the setal sac where it ends in the ganglion of the lateral organ. In the branchial region, the five pairs of lateral nerves pass between the bundles of oblique muscles. Minor branches of some of the lateral nerve pairs innervate the oblique muscle fibers. The ventral nerve cord is constricted to approximately

one third of its size as it passes through the thick ventral septum between the last branchial and first postbranchial segments.

The ventral nerve cord bifurcates at the posterior end of the last setigerous segment, sending a branch into each of the two ventral anal papillae.

Sense Organs. The sense organs have been described in another section. However, organs which can be classified as sensory organs include; nuchal organs, eyes, and lateral organs. In addition the palpode and anal papillae have been observed in living specimens to be highly sensitive to tactile stimuli. Aggregations of cells, such as the "branchial fenestrations" (see integumentary system) and the clusters of cells which send fibrous processes into the cuticle may also be classified as sensory organs (see figs. 52,53,54,55 and 76).

Discussion. The nervous system of the Opheliidae received considerable attention from various morphologists who worked in the late 19th century. Claparède (1869) and Pruvot (1885) briefly described the nervous system of Ophelia radiata. Meyer (1882) gave a detailed description of the nervous system of Polyopthalmus pictus. Kükenthal (1887) made a comparative morphological and histological study of the nervous systems of Travisia, Ophelia, Ammotrypane, Armandia, and Polyopthalmus, the most detailed and comprehensive of the papers published in that period. Descriptions of the nervous system of O. denticulata (as O. neglecta) were given by Schneider (1887) and de Saint-Joseph (1898). The most recent

publications, in which the opheliid nervous systems are described, include those by Brown (1938) and Hartmann-Schröder (1958). Hartmann-Schröder and Kükenthal both point out that the structure of the nervous system is very similiar in the various genera of the family Opheliidae. Kükenthal (1884) studied three species of Ophelia (O. radiata, O. limacina, and O. bicornis) and found that only slight differences occur in the structure of the nervous system of the three species.

The structure of the nervous system of the specimens of O. denticulata observed in this study is basically the same as that described by Kükenthal. However, there are two basic morphological differences between the nervous system of O. denticulata and that of O. radiata, as described by Kükenthal and Claparède. The brain of O. denticulata has an additional pair of branches, the occipital horns; also the ventral nerve cord gives off five pairs of nerves in each setigerous segment. In O. radiata occipital horns are lacking and ventral nerve cord gives off three pairs of nerves in each setigerous segment. My observations agree with those of Schneider concerning the structure of the brain of O. denticulata.

Hartmann-Schröder studied the nervous system of O. remanei in detail. Occipital horns are not present in O. remanei. The vacuolated cells found in the brain of O. denticulata are similiar to those described by Hartmann-Schröder for O. remanei. She suggests that the vacuolated cells may be neurosecretory cells.

Except for the fact that O. rathkei lacks occipital horns,

the morphology of the nervous system of O. rathkei, as described by Brown, is similiar to that of O. denticulata.

# SECTION V

## HABITS AND HABITAT

Habitat. The population of Ophelia denticulata, utilized for this study, is located in a sand bar approximately 250 yards west of the Hampton Harbor bridge in Hampton Beach, New Hampshire(70°49'13"W, 42°53'43"N.; fig. 80). The sand bar is crescent shaped with the two arms of the crescent facing the bridge. The sand bar is not directly exposed to the action of ocean surf but indirectly it is exposed to ocean swells, which are reduced in size by the jetties and shoal areas on the seaward side of the bridge. Strong westerly winds cause a sizeable "chop" in the harbor. Ebbing and flooding tides are "funneled" through the relatively narrow opening under the bridge. During the incoming tide, the tidal stream splits into two branches near the northerly arm of the sand flat. The northerly stream floods to the Hampton River side of the harbor. The southerly tidal stream flows nearly parallel to the east side of the sand bar and floods the Black Water Creek side of the harbor (Seabrook and Hampton Falls, New Hampshire). During the outgoing tide, the tidal flow from the Black Water Creek side of the harbor flows over the surface of the sand bar. The more northerly tidal flow joins the southerly current at the north side of the sand bar.

The average tidal range at Hampton Harbor is 7.8

feet. Correspondingly, the velocity of the peak tidal current is approximately 5-6 knots at the narrow outlet of the harbor near the bridge.

The effect of the tidal currents and wave action on the sand bar containing Ophelia is indicated by the physical condition of the sand. Ten sand samples were taken from the sand bar along a 100 yard line transect. The transect ran parallel to the easterly shore line near the low water mark where Ophelia collecting is best. Each of the samples was graded by running it through six sorting screens having mesh diameters of 1.981 mm., 1.0 mm., 0.5 mm., 0.246 mm., and 0.124 mm. For each sample, the amount of sand retained in each size class was weighed and recorded as a percentage of total sample weight. The data indicates that the sand is coarse. The amount of fine sand ($<0.25$ mm.) measured as a percentage of total sample weight, averaged 4.4% (average of 10 samples). Sand grains of larger diameter (between 0.25 mm. and 1.0 mm.) composed 94% of the total sample weight. Within the latter class, those having a diameter between 0.50 mm. and 1.0 mm. composed 61% of the total sample weight. The "black zone", when present, is usually deep and only occasionally comes near the surface. When it occurs, especially during the summer months, the "black zone" is located in the shallow drainage zone of the bar (see below) where the sand is finer (6.9%-7.2% fine sand). Large sand "waves", the crests of which lie

perpendicular to the shoreline of the bar, and more numerous, smaller sand ripples are common. Shallow drainage zones occur in the troughs of the sand waves. The sand bar has a gradual slope toward the shore line, without persistant surface pools.

Braefield (1964) has shown that the chief factor controlling the oxygen content of interstitial water seems to be revealed by the grain size analysis. The most significant correlation is between the oxygen content and the percentage of fine sand (<0.25 mm. diameter). If the amount of fine sand in a beach exceeds 10%, the oxygen content cannot rise above 20% of the air saturation level. There is no limit to the interstitial oxygen level if there is less than 10% fine sand. The reason for the correlation between the grain size and the oxygen content is the correlation between drainage time and oxygen content (Braefield, 1964). Drainage time is dependent upon grain size and distribution of grain size.

Amoureux (1962) has found that Ophelia bicornis requires a habitat of relatively high oxygen concentration (4-8 mg./l.). He suggested that the low oxygen concentration of the interstitial water is one of the principle reasons for the scarcity of O. bicornis along the French Coast. However, O. bicornis is found near rivers, zones of strong tidal currents, on well drained beaches of good slope, and where there is a good assortment of sand grains (Amoureux, 1962).

The sand bar at Hampton Beach, New Hampshire, in

which O. denticulata is found, is evidently one in which the oxygen content of the interstitial water can rise above 20% of the air saturation level. This ability to contain high concentrations of oxygen is probably one of the reasons for the occurrence of O. denticulata in this particular sand bar.

Population Density. The size of the population of Ophelia denticulata is difficult to determine because of its spotty distribution. Although the worms tend to cluster together in certain parts of the sand bar, there are seldom more than 8-10 worms in the largest of clusters. The density of the population of O. denticulata is not as great as that of O. rathkei, as reported by Brown (1936) and Scott (1961). Nor is it as dense as the population of O. bicornis located in zones II and III at the mouth of the Horn River and the Guillec River near Roscoff, France (Amoureux, 1962).

Local Distribution. Clusters of O. denticulata are always found in a particular association with the large sand "waves". Each sand wave is oriented perpendicular to the shore line. In cross section, the sand wave has a long slope of increasing height to the crest where it drops off sharply to the trough. The crests become flattened and the trough broader and shallower near the mean low water mark. There are usually six to eight sand waves on the sand bar. Clusters of O. denticulata are located: 1. in the trough on the steep slope beneath the crest; 2. on the beginning of the gradual slope which goes to the next crest; 3. and on the

flattened crest near the low water mark. In addition, scattered individuals are located in the trough of small sand ripples where the sand is not too coarse to hold some moisture during low tide.

Burrowing. There is no visible indication of the presence of O. denticulata on the sand bar, such as tubes, or castings. When placed on the surface of the sand, the worm usually lies on its side, coiled in a flat spiral, with its "head" tucked into the ventral groove of the posterior segments. It may remain motionless for a few minutes or it may begin a writhing movement prior to burrowing. Copious amounts of mucus are secreted along the dorsal midline and in the region of the parapodia. While the worm is writhing, sand grains accumulate in the bands of mucus. By alternately expanding and contracting the prebranchial region, especially those segments anterior to the injector organ, the worm forces the sand grains aside and burrows beneath the surface. Most of the mucus, which may act as a lubricant during the burrowing process, is left on the surface of the sand.

Co-inhabitants. The following is a list of species of various phyla of animals which have been collected in the sand bar in which Ophelia denticulata lives. Their abundance is indicated only generally by the terms "rare" or"common".

Polychaeta - Nephtys bucera - common
N. caeca - rare
Scolelepis squamata - common

| | |
|---|---|
| Nemertea - | *Micrura leidyi* (?) - common |
| | *Cerebratulus lacteus* - rare |
| Mollusca | |
| Pelecypoda | *Mesodesma arctatum* - common |
| | *Spisula solidissima* - rare |
| Gastropoda | *Lunatia heros* - rare |
| Arthropoda | |
| Crustacea | |
| | *Haustorius* sp. - common (amphipod) |
| others | nematodes<br>dinoflagellates (*Amphidinium* sp.).<br>ciliates<br>diatoms |

# SECTION VI

## SUMMARY

The taxonomic and morphological characters of the opheliid polychaete Ophelia denticulata, found in a coarse, shifting sand bar at Hampton Beach, New Hampshire, in addition to a study of its internal anatomy are presented in this thesis.

It was found that, although Verrill first collected Ophelia denticulata off Block Island, Rhode Island in 1875 and subsequent collections of this species were made in Pouliguen, France, Hampton Beach, New Hampshire, and Cape Hatteras, North Carolina, only the papers by de Saint-Joseph (1898) and Schneider (1887) included sections about the anatomy of O. denticulata.

A sand particle analysis and other factors such as the presence of sand ripples and strong tides indicate that the sand bar, in which the population of O. denticulata is found, is well aerated.

The following systems and organs were studied: circulatory, nervous, alimentary tract, musculature, nephridia, and integument. The structure of the circulatory system of Ophelia denticulata is similiar to that of Ophelia radiata as described by Schaeppi. A major point of difference occurs in the interpretation of the direction

of blood flow and whether or not a connection between the subintestinal ventral vessel and the intestinal sinus exists. No connection between the vessel and the sinus could be found in O. denticulata. In O. denticulata, the blood flows anteriorly in the intestinal sinus and dorsal blood vessel and posteriorly in the anterior ventral vessel and posterior ventral vessel. Blood flows from the posterior ventral vessel into the intestinal sinus through the branchial (ventral and dorsal segmental) vessels. Blood, propelled by contractions of a dorsal heart, flows into the dorsal vessel and through the circumgastric vessels into the subintestinal ventral vessel. There are numerous blind vessels, associated with the segmental and intersegmental vessels in O. denticulata as well as in other species of Ophelia.

There are three major groups of muscles; longitudinal, circular, and oblique. The areas where the oblique muscles attach to the body wall are pulled inward resulting in the characteristic lateral and ventral grooves. The muscular ligaments, attached to the ventral and dorsolateral regions of the stomach and intestine, support the gut. Muscle bands associated with the pharynx, setal sacs, nuchal organs, and lateral organs are described.

Two types of nephridia are described. The more anterior pairs are located in the third through the eighth branchial segments. The posterior pairs, morphologically

different, are located in the remaining branchial segments. A discussion of the possible functions of the two types of nephridia is given.

The integument is composed primarily of an outer cuticle, the epidermis, and the basement membrane. The epidermis is composed of two types of support cells and three types of gland cells. Gland cell packets, with one or more types of gland cells, each open to the outside through a single pore. Cuticular invaginations either anchor the cuticle to the epidermis or serve as sites of attachment for the thick oblique muscle bands in the branchial region.

The cerebral ganglion is located in the posterior part of the palpode. Occipital horns, nuchal organ nerves, gangliiform nerves, and the circumpharyngeal connectives are structures associated with the brain of O. denticulata. Lateral organs, located between the noto- and neuropodia in each setigerous segment, are directly innervated by a major nerve branch of the ventral nerve cord. In each setigerous segment, the ventral nerve cord gives off five pairs of lateral nerves.

The alimentary tract is divisible into five regions; eversible pharynx, esophagus, stomach, intestine, and rectum. The histological structure of each of the regions is described. A midventral fold of the gut, the typhlosole, occurs in the stomach and intestine. Additional lateral

folds also occur in the stomach. As in Euzonus (Thoracophelia) mucronata, three rectal ciliated organs are present in O. denticulata.

The taxonomy and taxonomic characters of the family Opheliidae and of the genus Ophelia are reviewed. A critical study of the taxonomic characters presently utilized in defining species of Ophelia (primarily number and location of branchiae) reveals that less variable characters such as origin of ventral grooves and shape of the posterior end should also be used. Bellan's taxonomic study of Ophelia bicornis and the various forms of Ophelia radiata located in the Mediterranean Sea is based primarily on the number and location of branchiae. As a result of his study, Bellan is convinced that O. bicornis and O. radiata are conspecific. Preliminary studies of O. bicornis collected at Georgetown Island, Maine, O. bicornis and O. radiata from the United States National Museum, based on the origin of the ventral groove and location of the glandular ridge, indicate that the two are probably separate species.

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# Key to Symbols used on Figures

aBrBV, afferent branchial vessel
Agl, type A gland
An, annuli
APd, dorsal anal papillae
APv, ventral anal papillae
AV, anal valve
AVP, anal valve papillae
Bgl, type B gland
BlBV, blind blood vessels
Bm, basement membrane
Br, branchiae
BrB, brush border
Brcp, branchial capillaries
Brf, branchial fenestrations
Brn, brain
BuS, buccal segment
BV, blood vessel
BW, body wall
Cct, coelomocyte
Cepi, coelomic epithelium
Cg, chloragogen
Cgl, type C gland
Cil, cilia
CilEpt, ciliated epithelium
CilgrV, ciliated ventral groove
CilO, ciliated organ
CM, circular muscles
CmGaBV, circumgastric vessel
Coe, coelom
Com, commissures
CphCon, circumpharyngeal connective
CphConCom, circumpharyngeal conn. commissure
CT, connective tissue
Cu, cuticle
D, dorsal
DBV, dorsal blood vessel
DLM, dorsal longitudinal muscles
DNT, descending nephridial tubule
DSV, dorsal segmental vessel
eBrBV, efferent branchial vessel
Epd, epidermis
Ept, epithelium
Es, esophagus
Ey, eye
Ft, fiber tract
GaP, gastric pouch
Ga typh, gastric typhlosole
Gfn, gangliiform nerve
Gl, gland
GlR, glandular ridge
GrL, lateral groove
GrPO, postoral groove
GrPrO, preoral groove
GrV, ventral groove
Hb, heart body
HNT, horizontal nephridial tubule
Ht, heart
InO, injector organ
Int, intestine
Int typh, intestinal typhlosole
IsBV, and IsVBV, intersegmental blood vessel
LM, longitudinal muscle
Lp, labial pit
LtO, lateral organ
$LtO_1$, neuropodial postsetal lobe (extension of lateral organ)
LtR, lateral ridge
M, mouth
Mp, protractor muscle
Mr, retractor muscle
Ne, neuropodium
Neph, nephridium
NeS, neuropodial setae
Neu, neuron
NO, notopodium
NOCom, nuchal organ commissure
NOn, nuchal organ nerve
NoS, notosetae
Np, neuropile
NPR, nephridiopore
NST, nephrostome
NSTl, nephrostomial lip
Nu, nucleus
NuO and NO, nuchal organ
OccH, occipital horn
OM, oblique muscle
Pa, parapodium
Pd, palpode
PbMr, proboscis retractor muscle
Pdn, pedal nerve
Pe, peritoneum
Ph, pharynx
Ph(Pb), pharynx(proboscis)

Po, pore
PreL, presetal lobe
Prob, proboscis
Ps, prostomium
Re, rectum
Rtyph, rectal typhlosole
SbIntVBV, subintestinal ventral blood vessel
Sc, support cell
Sep, septum
SEs, esophageal sinus
Set, setigerous segment
SGa, gastric sinus
SgVBV, subgastric ventral blood vessel
SInt, intestinal sinus
SLi, suspensory ligament
SRe, rectal sinus
SS, setal sac
SSM, setal sac muscles
St, stomach
Stg, stomatogastric nerve
S typh, typhlosolar sinus
typh, typhlosole
TyphV, typhlosolar vessel
V, ventral
VBV, ventral blood vessel
VBVa, anterior ventral vessel
VBVa-L, lateral branch of anterior ventral vessel
VBVa-M, medial branch of anterior ventral vessel
Vc, vacuole
Ve, vesicles
VLM, ventral longitudinal muscles
VNC, ventral nerve cord
VSV, ventral segmental vessel

TABLE I

COMPARISON OF OPHELIA SPECIES OF THE BICORNIS GROUP

| | O. bicornis | O. denticulata | O. radiata** | O. bipartita | C. dannevigi |
|---|---|---|---|---|---|
| Body Formula* | 10a+15b(2b-7b)+7a=32 | 9a+18b(3b-8b)+5a=32 | 10a+14b(2b-7b)+8a=32 | 9a+17b(3b-8b)+5a+1=32 | 10a+19b(-)+3a=32 |
| Origin Ventral Groove | Setiger 10 (jct. 9-10) | Setiger 10 (jct. 9-10) | Setiger 11 (jct. 10-11) | Setiger 9 (jct. 8-9) | Setiger 10 (?) |
| Glandular Ridge | Setiger 9 | Setiger 9 | Setiger 10 | (-) | (-) |
| Branchial Fenestrations | (-) | (+) | (-) | (+) | (?) |
| Nephridiopores | 6 Pr. Setiger 12-17 | 6 Pr. Setiger 12-17 | 5 Pr. Setiger 12-16 | 6 Pr. Setiger 12-17 | (?) |
| Anal Papillae (Ventral) | 2 -Lanceolate | 2 -Lanceolate | 2 -Lanceolate | 2 -Lanceolate | 2 -Lanceolate |
| Shape Posterior End | Truncated | Truncated | Truncated | (?) | Truncated |
| Location 1st. Pair Branchiae | Variable Never Set. 10 | Setiger 10 (1 st. Abd. Seg.) | Setiger 11 (1 st. Abd. Seg.) | Setiger 10 (2 nd. Abd. Seg.) | (?) (Possibly 2 nd. Abd. Seg.) |

*From Tebble 1953

**Examination of specimens in U. S. N. M., catalogue number 5138

TABLE IIa

COMPARISON OF THE SPECIES OF THE LIMACINA-GROUP

| | O. limacina | O. roscoffensis | O. africana | O. agulhana | O. capensis |
|---|---|---|---|---|---|
| Body formula | 10a+22b(2b-7b)+7a=32 | 8a+23b(4b-9b)+1a=32 | 9a+18b(3b-8b)+2a+2n=31 | 9a+25b(3b-8b)+2a+2n=37 | 10a+19b(-)+3a+3n =35 |
| Shape posterior end | Taper | Taper | Taper | Taper | Taper |
| Origin ventral groove | Setiger 8 (jct. 7-8) | Setiger 8 (jct. 7-8) | Setiger 8 (jct. 7-8) | Setiger 7 | (?) |
| Nephridiopores | 6 pr. | 6 pr. | 6 pr. | 6 pr. | (?) |
| Glandular ridge | (-) | (-) | (-) | (-) | (-) |
| 1 st. Pr. branchiae | Setiger 11 (4 th. abd. seg.) | Setiger 9 (2 nd. abd. seg.) | Setiger 10 (3 rd. abd. seg.) | Setiger 10 (3 rd. -4th. abd. seg.) | Setiger 11 |
| Anal papillae | Digitiform | Digitiform Dorsal group vestigial | Digitiform | Digitiform small | Digitiform small |
| Branchial fenestrations | (+) | (-) | (+) | (+) | (+) |
| Postbranchial dorsolateral grooves | Inconspicuous Last 3 setigers | Large Single on Setiger 28-29;double on setigers 30-33 | Inconspicuous On segments 40, 41, and pygidium | Large Last 5-6 segments Crimped | Large Last 9-10 segments |

TABLE IIb

COMPARISON OF THE SPECIES OF THE LIMACINA-GROUP

| | O. formosa | O. magna | O. pulchella | O. praetiosa |
|---|---|---|---|---|
| Body formula | 9a+26b(3b-8b)+6a=41 | 10a+31b(-)+5a=46 | 9a+24b(3b-8b)+5a=38 | 8a+18b(4b-9b)+5a=31 |
| Shape posterior end | Taper | Taper | Taper | (?) |
| Origin ventral groove | (?) | Setiger 8 (jct. 7-8) | (?) | (?) |
| Nephridiopores | 6 pr. (setiger 12-17) | (?) | 6 pr. (setigers 12-17) | 6 pr. (Setigers 12-17) |
| Glandular ridge | (-) | (-) | (-) | (-) |
| lst. pr. branchiae | Setiger 10 | Setiger 11 (4th. abdominal seg.) | Setiger 10 | Setiger 9 |
| Anal papillae | (?) | Digitiform knobbed | (?) | (?) |
| Branchial fenestrations | (+) | (+) | (+) | (?) |
| Postbranchial dorsolateral grooves | Inconspicuous On postbranchial segments | conspicuous Last 5 segments | conspicuous Last 4 posterior segments | (?) |

TABLE III

COMPARISON OF GENERA OF THE FAMILY OPHELIIDAE

| | | Location of branchiae | Shape of branchiae | Lateral eyes | Subdivisions of Body | Pygidium | Body form |
|---|---|---|---|---|---|---|---|
| Group I | Ammotrypane | from setiger 2 | cirriform | (-) | none | anal tube<br>1 medial cirrus<br>2 lg. papillae | elongate, narrow (Amphioxus) |
| | Armandia | from setiger 2 | cirriform | 10-12 pairs from setiger 7 | none | anal funnel<br>11 papillae and<br>1 medial cirrus | elongate, narrow (Amphioxus) |
| | Polyopthalmus | none | none | (+) | none | anal tube with papillae | elongate, narrow (Amphioxus) |
| | Ammotrypanella | posterior region only | cirriform | (-) | none | elongate anal tube | ? |
| | Antiobactrum | present | cirriform | ( -) | none | short anal tube | ? |
| Group II | Trachytrypane | none | none | (-) | none | short anal tube, papillae lacking | elongate, narrow (Ascaris) |
| Group III | Ophelia | posterior two-thirds | cirriform | (-) | 2-3 thoracic, abdom., (caudal) | 0, 1, 2 ventral anal papillae | (-) |
| | Euzonus (Thoracophelia) | posterior two-thirds | twin filament | (-) | same * | 1 ventral anal papilla | (-) |
| | Euzonus (Euzonus) | posterior two-thirds | dendritic or pectinate | (-) | same * | same | (-) |
| Group IV | Travisia | from setiger 2 | cirriform | (-) | 2;anterior = round. Post. = rectangular | button shaped | grub-like |
| | Kesun | none | none | (-) | same | cylindrical, longitudinally furrowed | grub-like |

* second setiger enlarged

Figure 1. Lateral view of Ophelia denticulata Verrill 1875

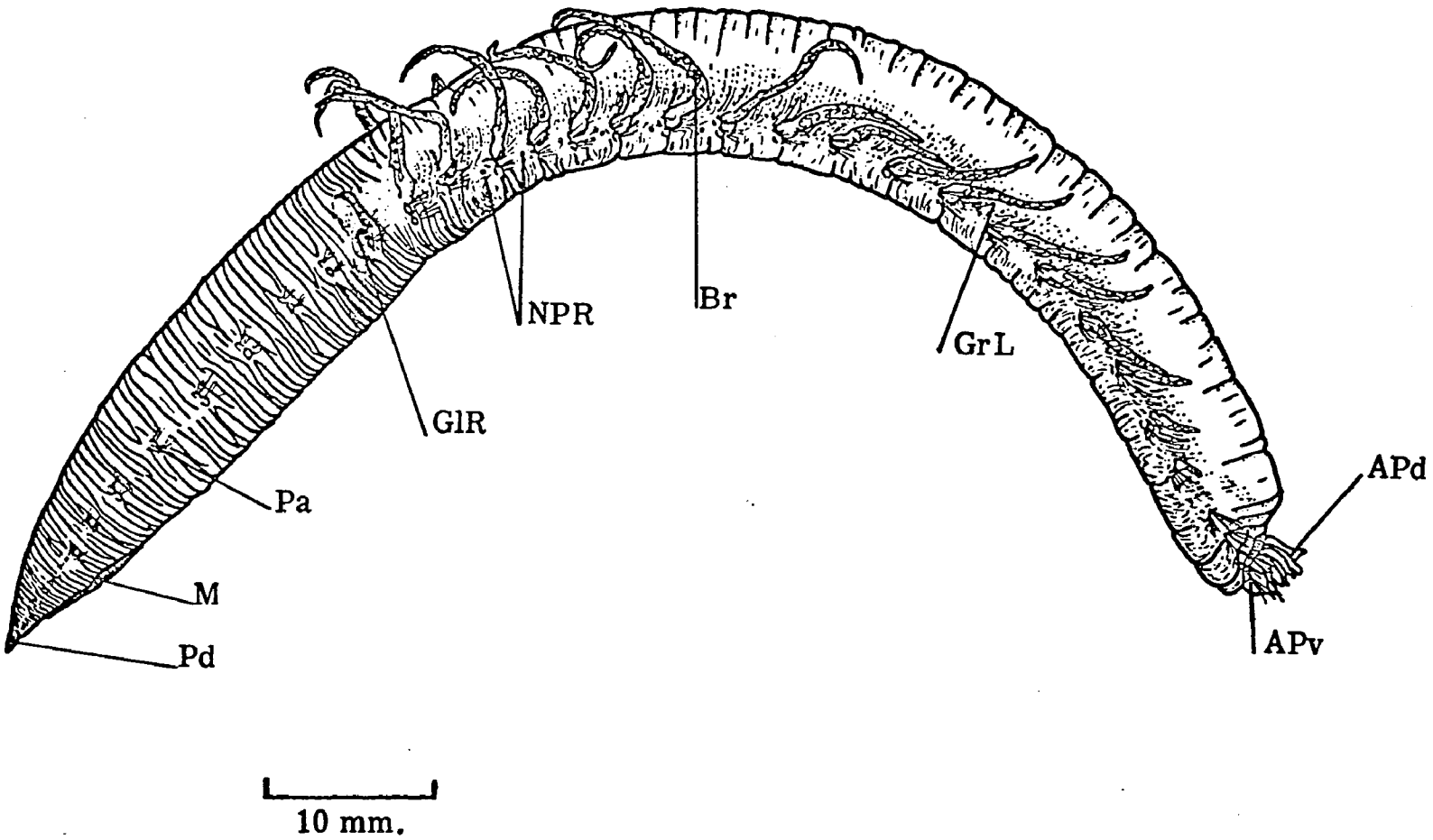


Figure 1

Figure 2. Lateral view of prostomium, peristomium, and setigerous segments 1,2, and 3.

Figure 3. Dorsal view of prostomium, peristomium, and setigerous segment 1.

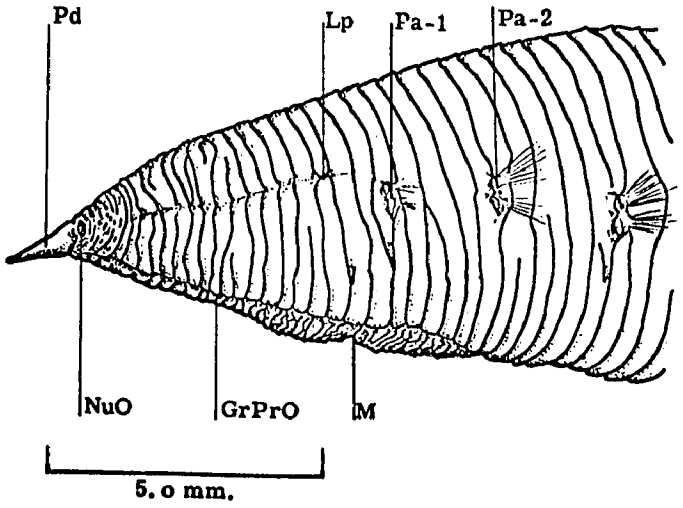


Figure 2

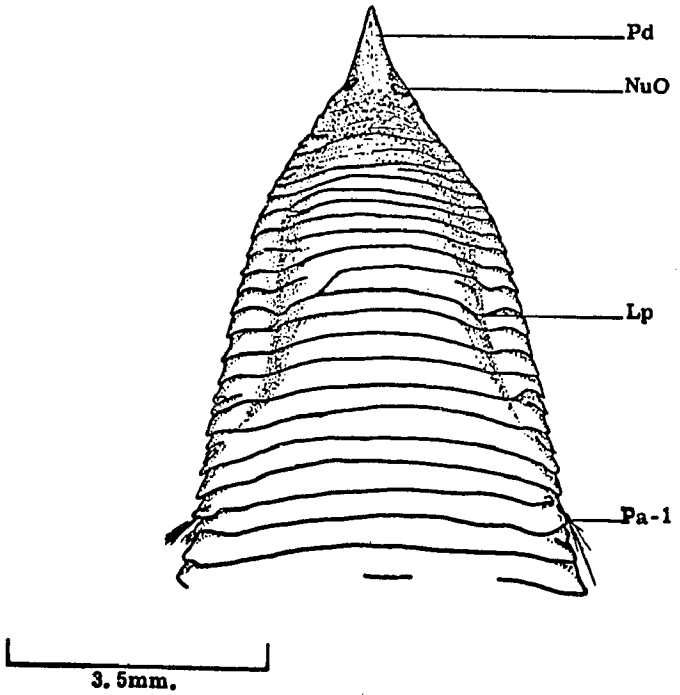


Figure 3

Figure 4. Ventral view of prostomium, peristomium, and setigerous segment 1.

Figure 5. Lateral view of anterior portion of branchial region.

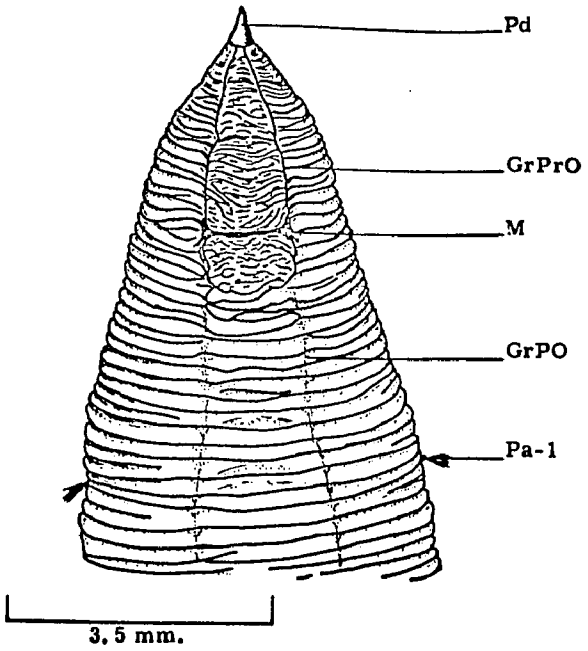


Figure 4

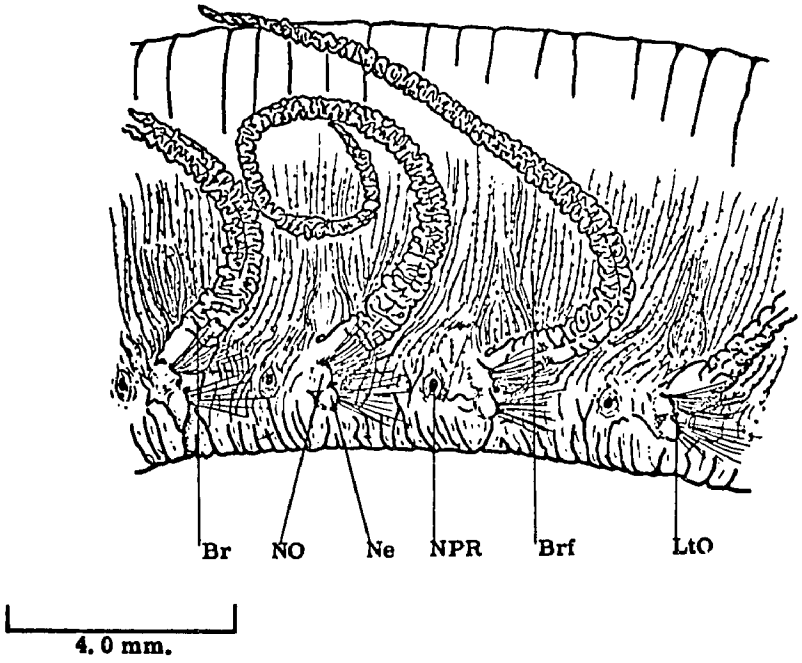


Figure 5

Figure 6. Lateral view of postbranchial region. Setiger 28 is the first postbranchial segment.

Figure 7. Dorsal view of postbranchial region.

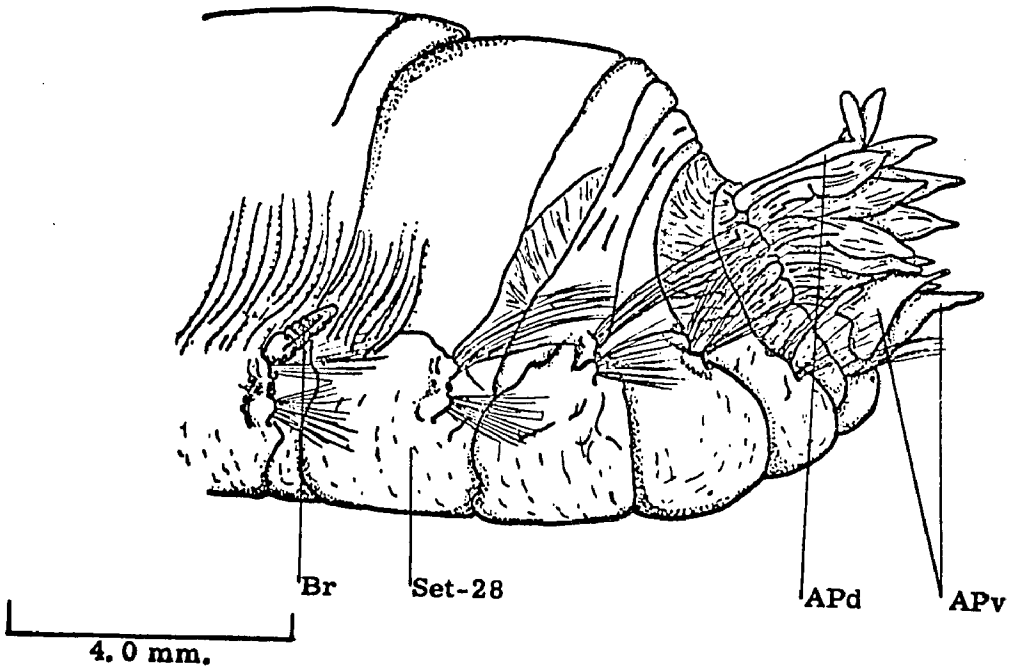


Figure 6

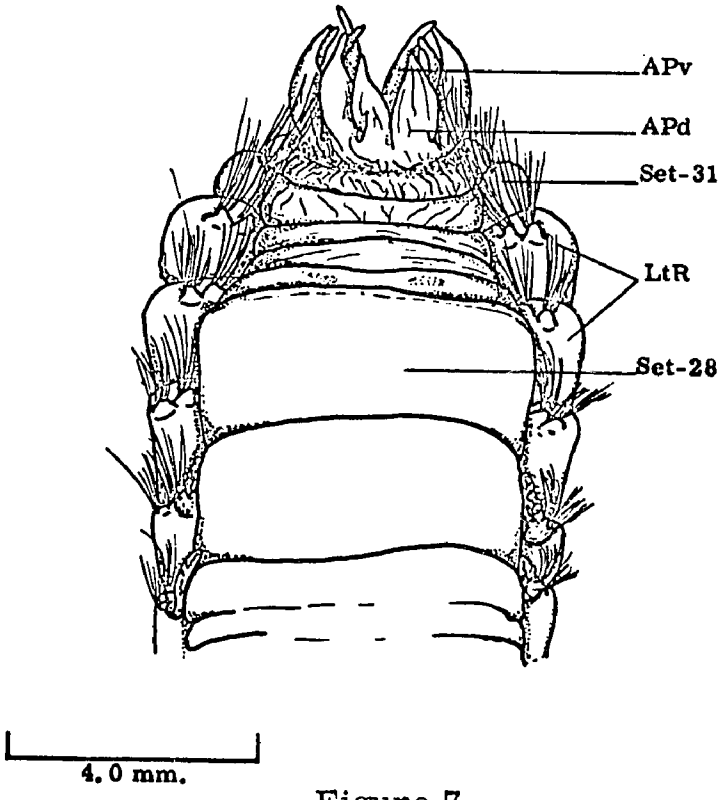


Figure 7

Figure 8. Ventral view of postbranchial region. Note: Ventral groove.

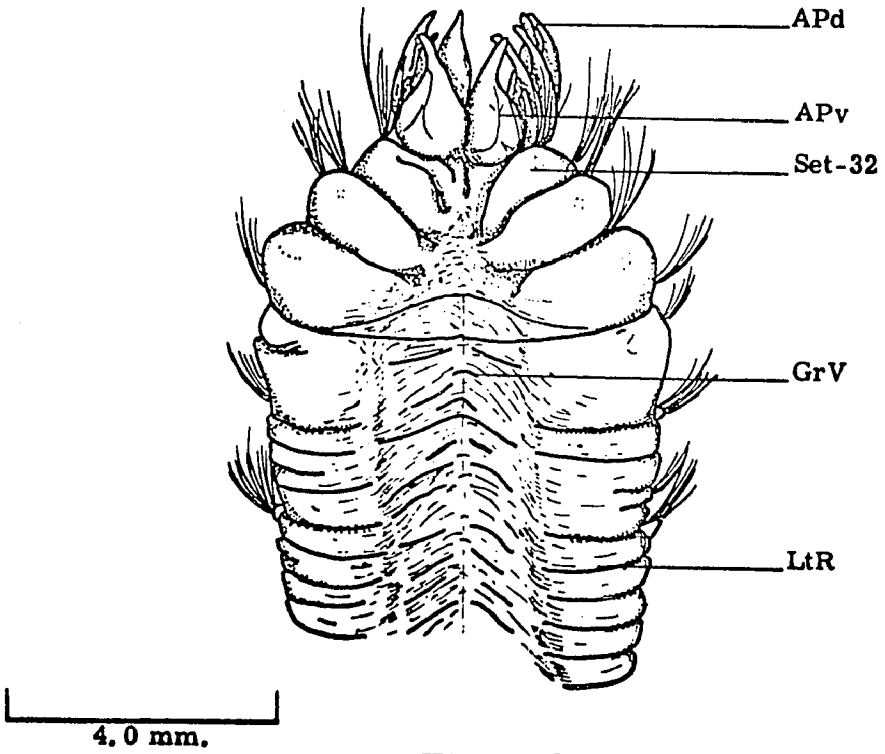


Figure 8

Figure 9. Diagram of the major vessels and sinuses of the circulatory system. Lateral view.

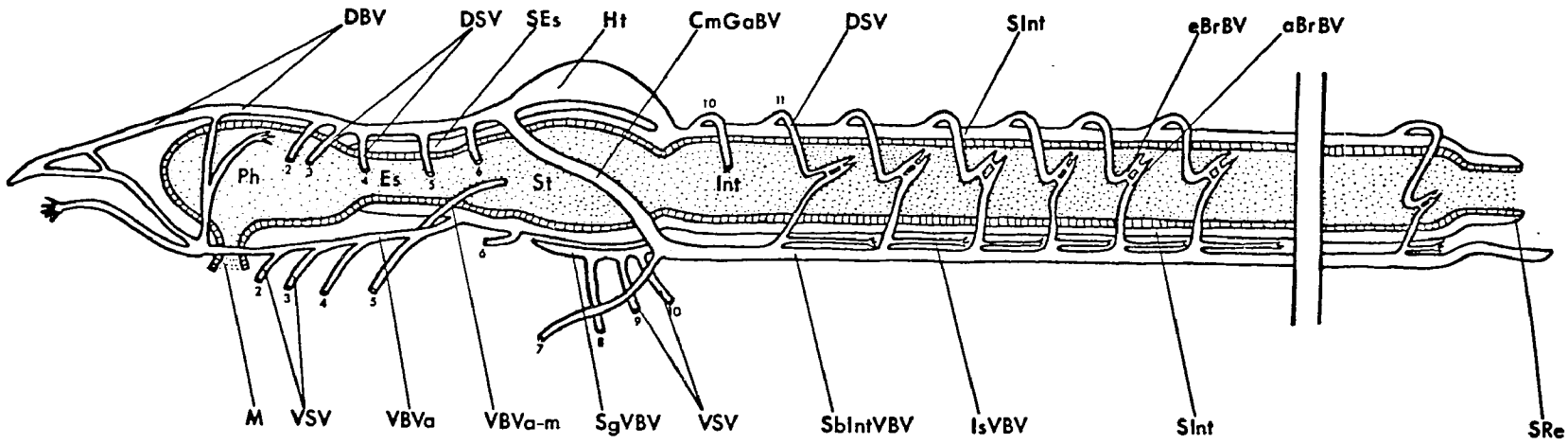
DBV
DSV
SEs
Ht
CmGaBV
DSV
SInt
eBrBV
aBrBV
Ph
Es
St
Int
M
VSV
VBVa
VBVa-m
SgVBV
VSV
SbIntVBV
IsVBV
SInt
SRe

Figure 9

Figure 10. Cross section of gut at junction of stomach and intestine. Origin of gastric pouches.

Figure 11. Cross section of anterior part of intestine. Intestinal sinus separated from gastric pouches.

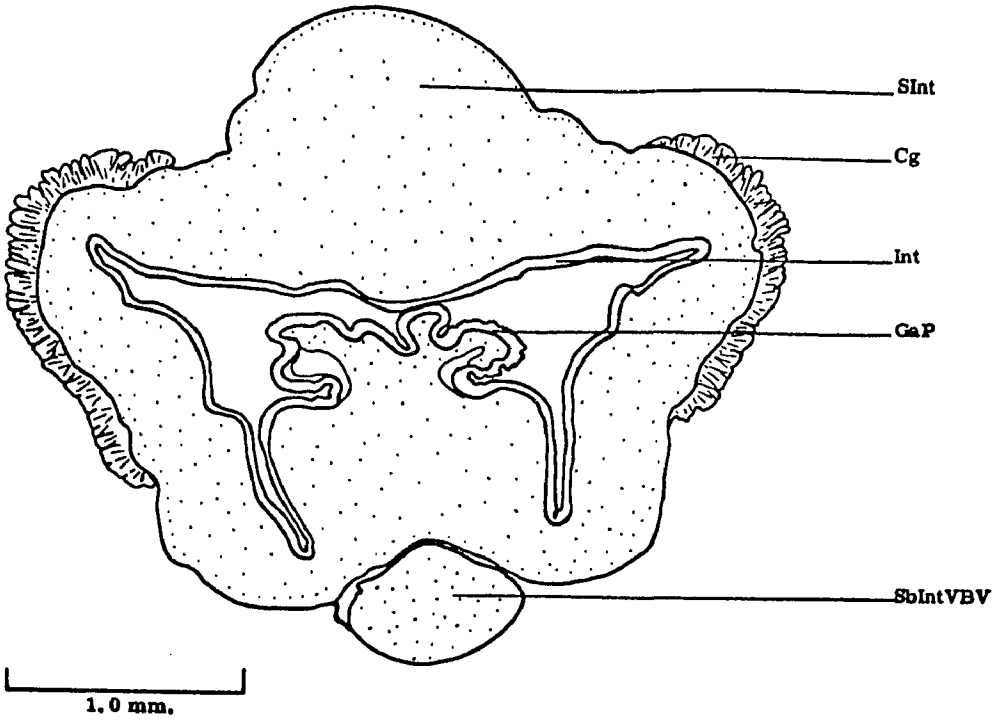


Figure 10

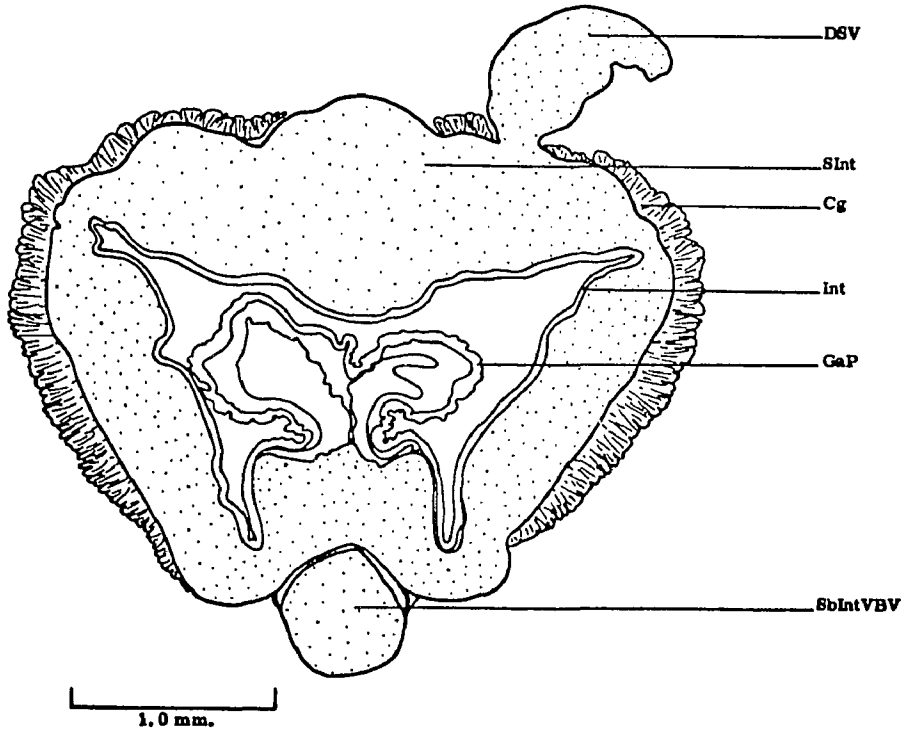


Figure 11

Figure 12. Cross section of anterior part of intestine. Interior of gastric pouch is continuous with coelom.

Figure 13. Cross section of anterior part of intestine. Gastric pouches separated from floor of intestine. Note: typhlosolar vessels.

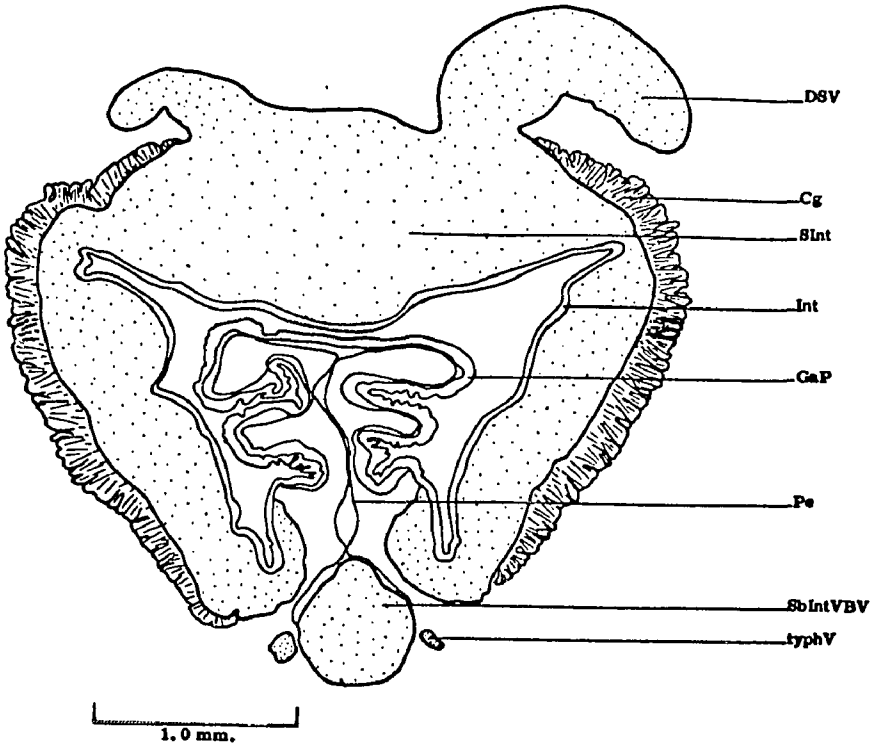


Figure 12

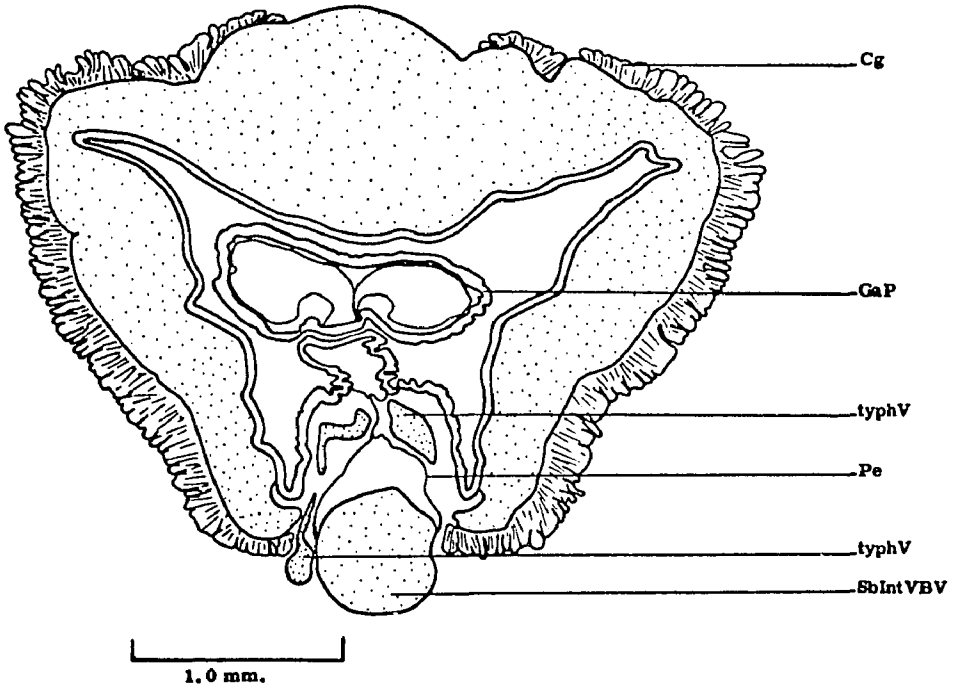


Figure 13

Figure 14. Cross section of anterior part of intestine. Origin of intestinal typhlosole.

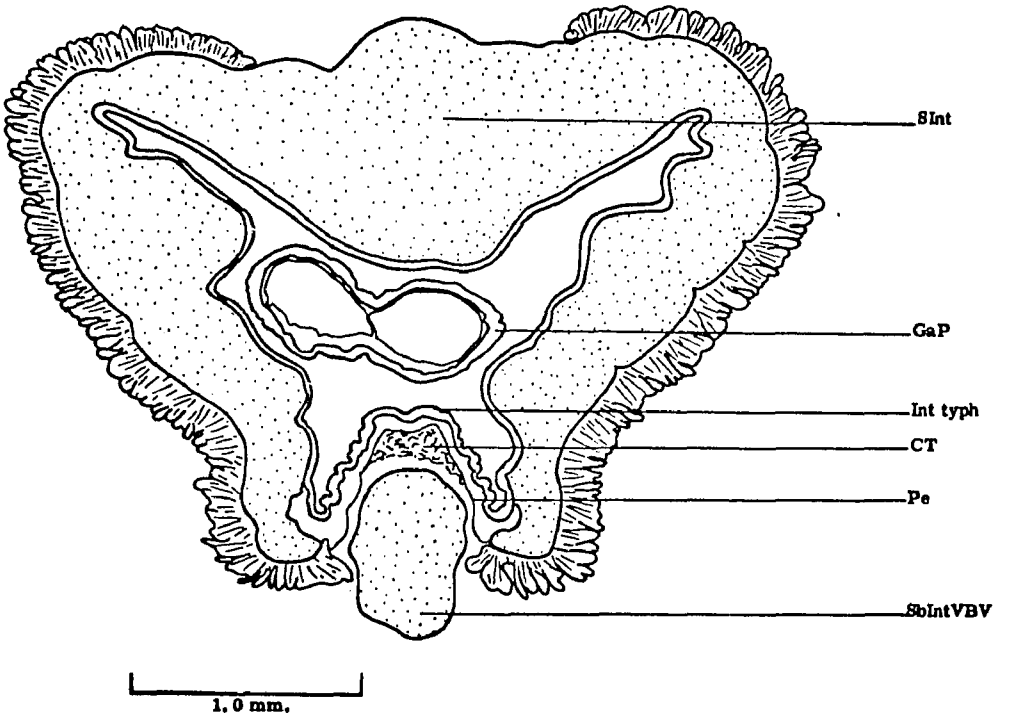


Figure 14

Figure 15. Cross section of prebranchial region indicating the relationship between the esophagus and the three branches of the anterior ventral blood vessel.

Figure 16. Cross section of prebranchial region. The three branches of the anterior ventral blood vessel are united.

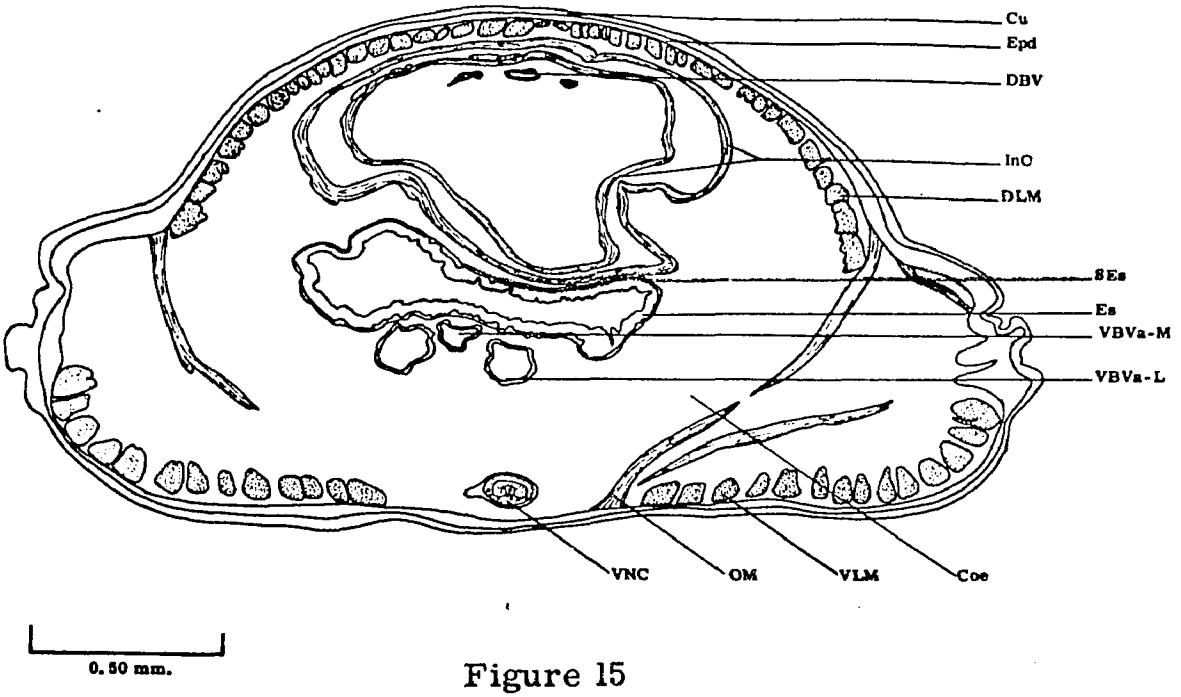


Figure 15

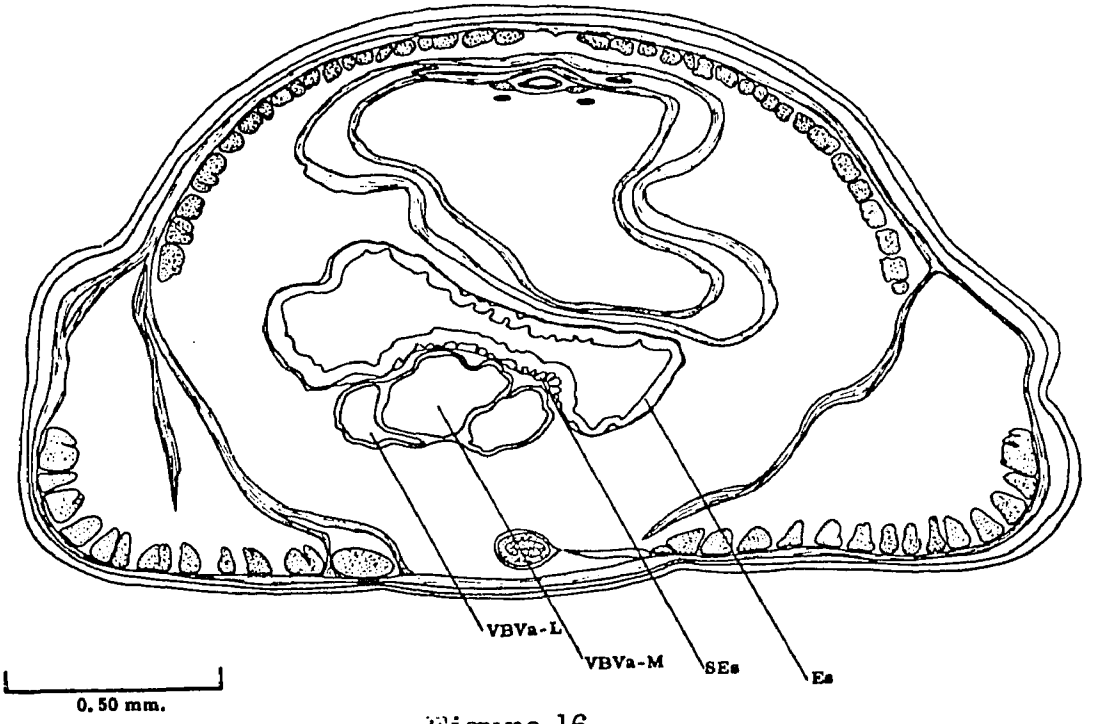


Figure 16

Figure 17. Cross section of prebranchial region. Union of lateral branches of anterior ventral blood vessel with the esophageal sinus. Incorporation of medial branch of anterior ventral blood vessel into the typhlosole at junction of esophagus and stomach.

Figure 18. Cross section of prebranchial region. Origin of gastric typhlosole and lateral fold of stomach.

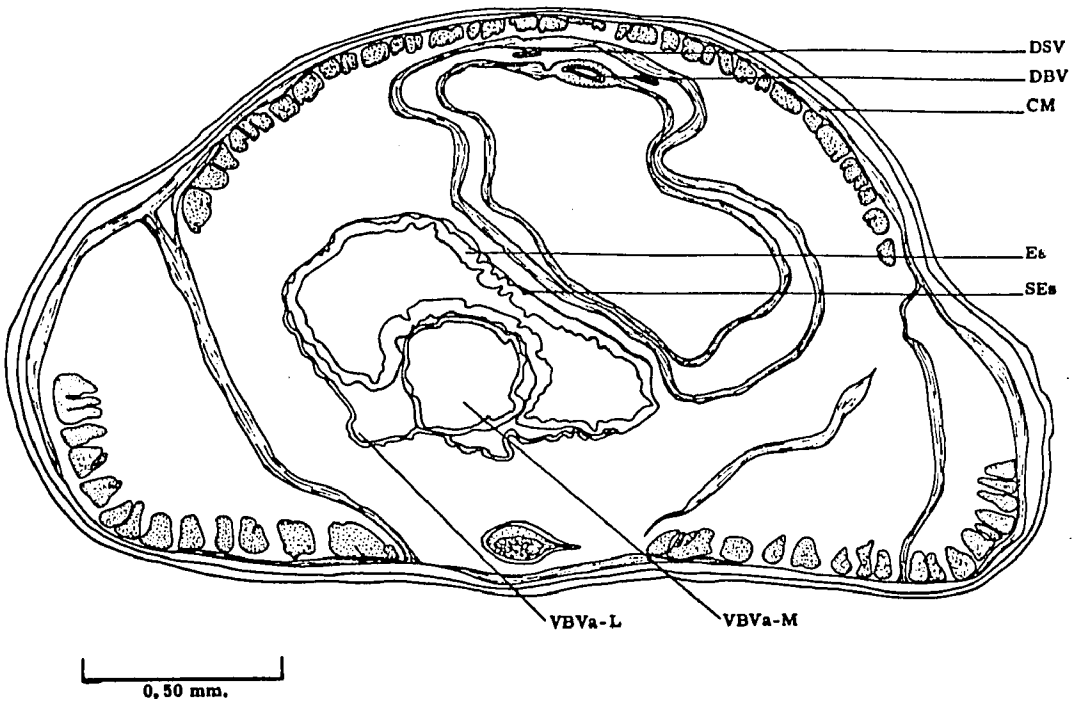


Figure 17

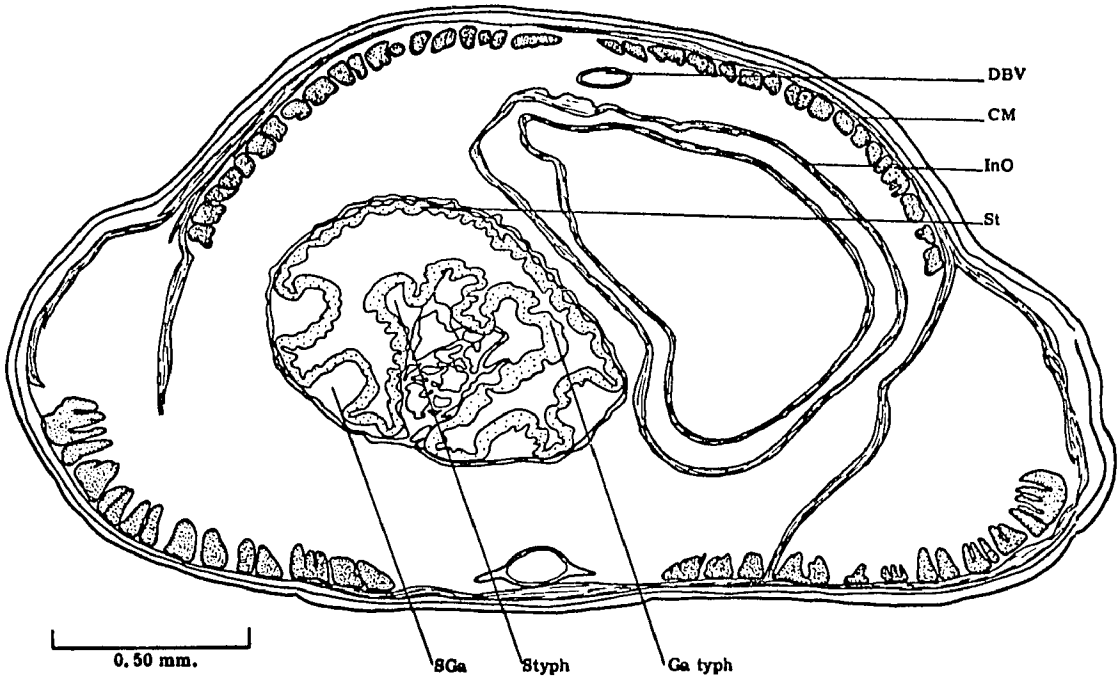


Figure 18

Figure 19. Cross section of prebranchial region. Increased folding of gastric typhlosole and wall of stomach.

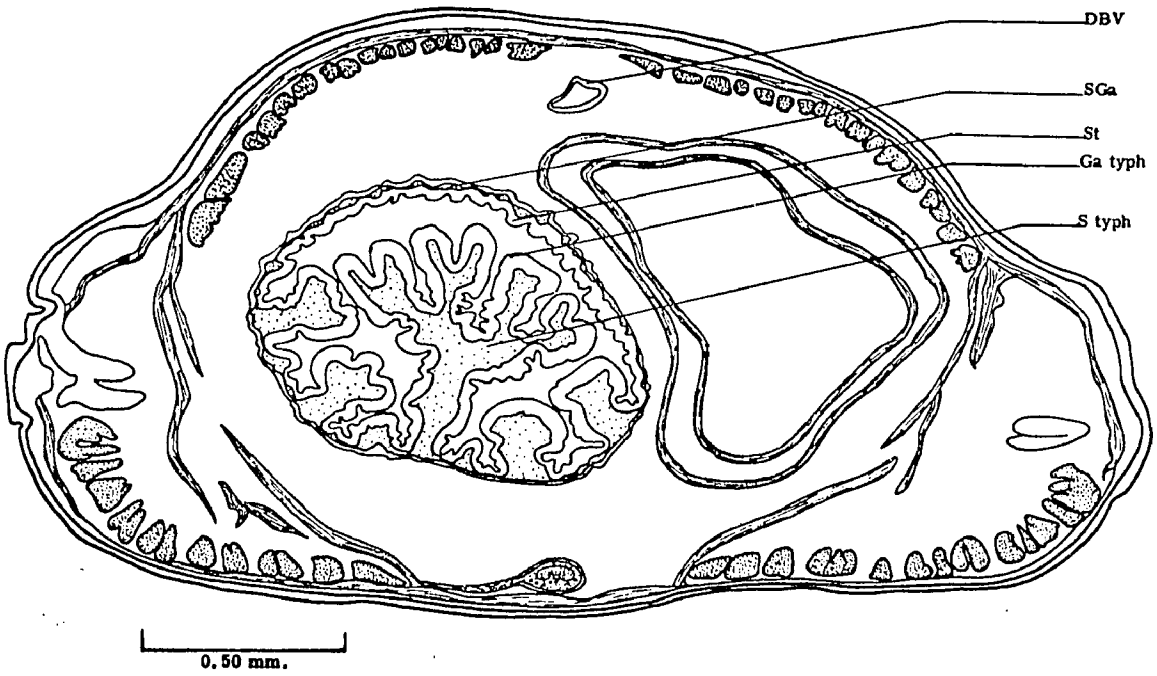


Figure 19

Figure 20. Cross section at junction of prebranchial and branchial regions. Ventral union of circumgastric vessels forming the subintestinal ventral blood vessel.

Figure 21. Cross section at junction of prebranchial and branchial regions. Subintestinal ventral blood vessel formed. Thickened oblique muscle bands.

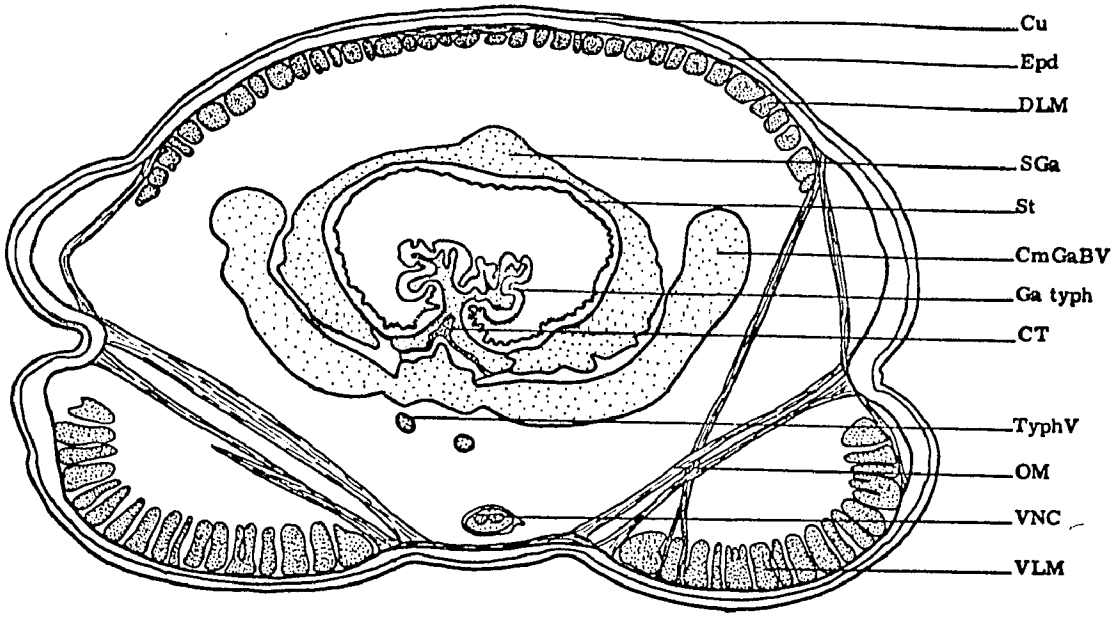


Figure 20

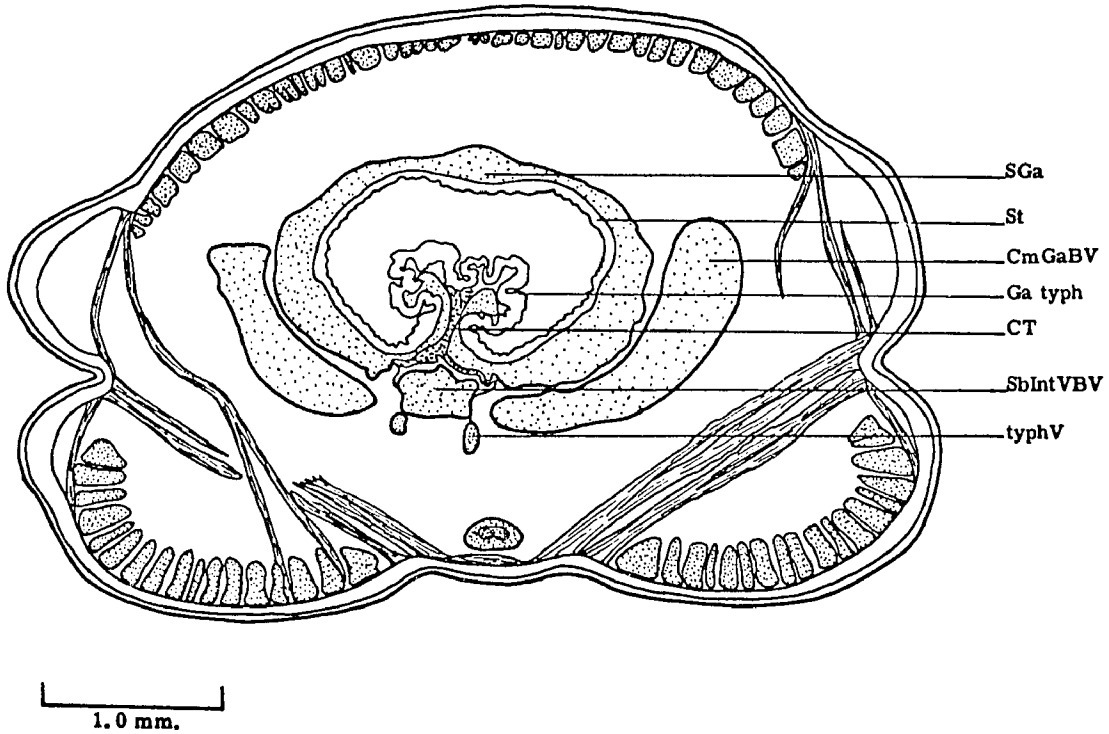


Figure 21

Figure 22. Cross section of anterior part of branchial region. Formation of ventral and lateral grooves at points of attachment of oblique muscle bands.

Figure 23. Cross section of branchial region. Intestinal typhlosole continuous with the intestinal sinus. Chloragogen cells within the intestinal typhlosole. Ventral nerve cord moved upward by the oblique muscles.

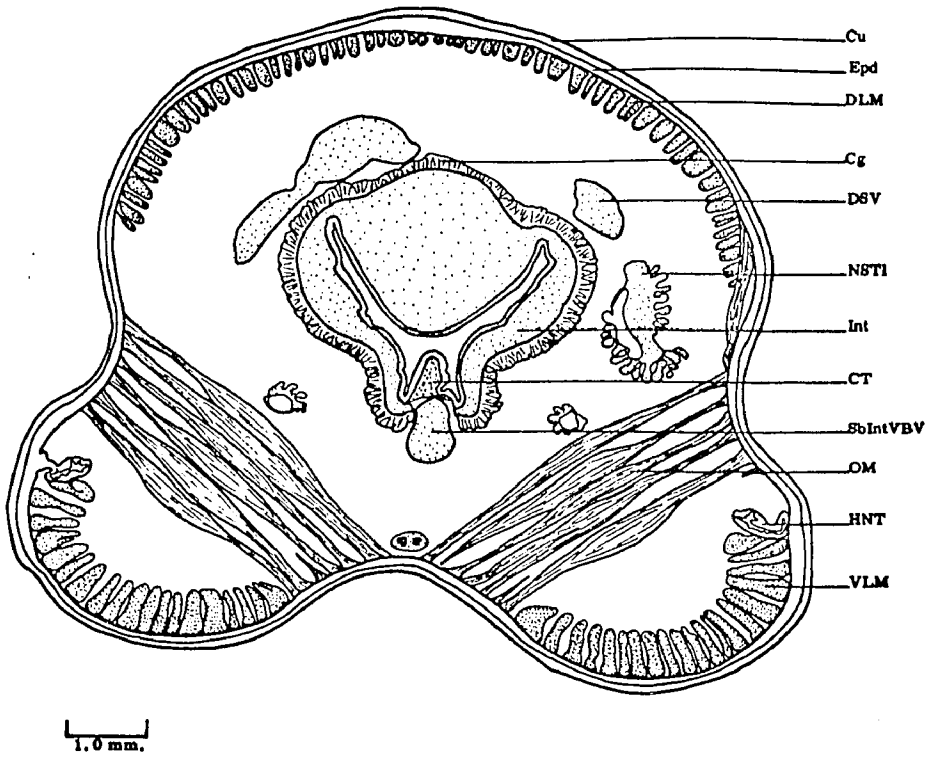


Figure 22

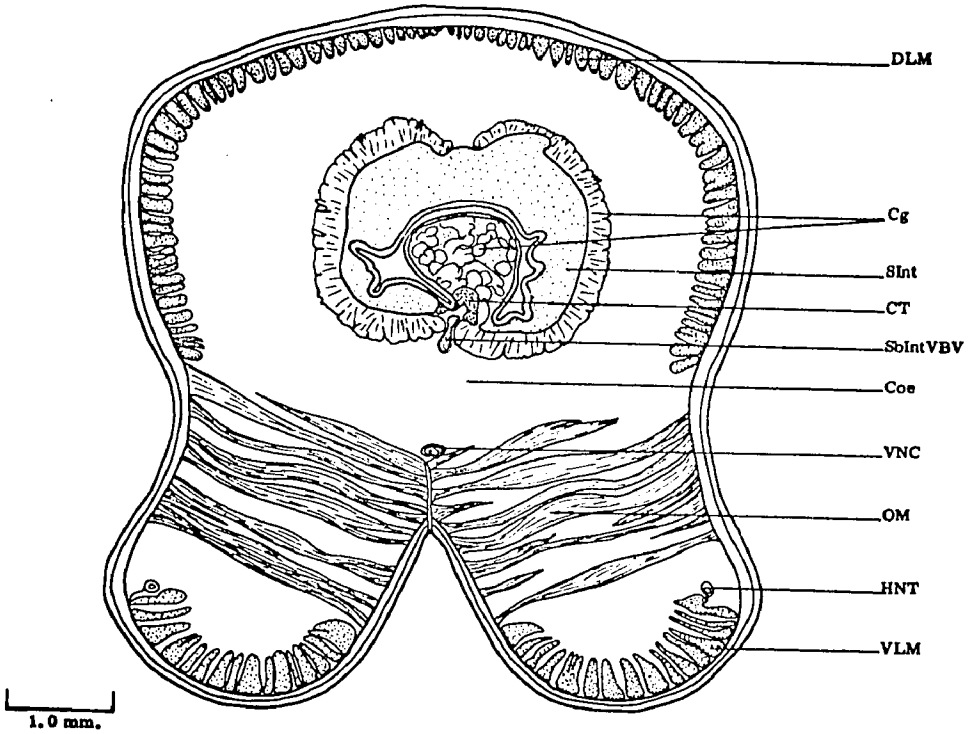


Figure 23

Figure 24. Cross section of postbranchial region. Two ciliated organs in the dorsal wall of rectum and one in the anal valve.

Figure 25. Cross section of postbranchial region. Modified circular and oblique muscle bands attach to epidermis and to wall of rectum.

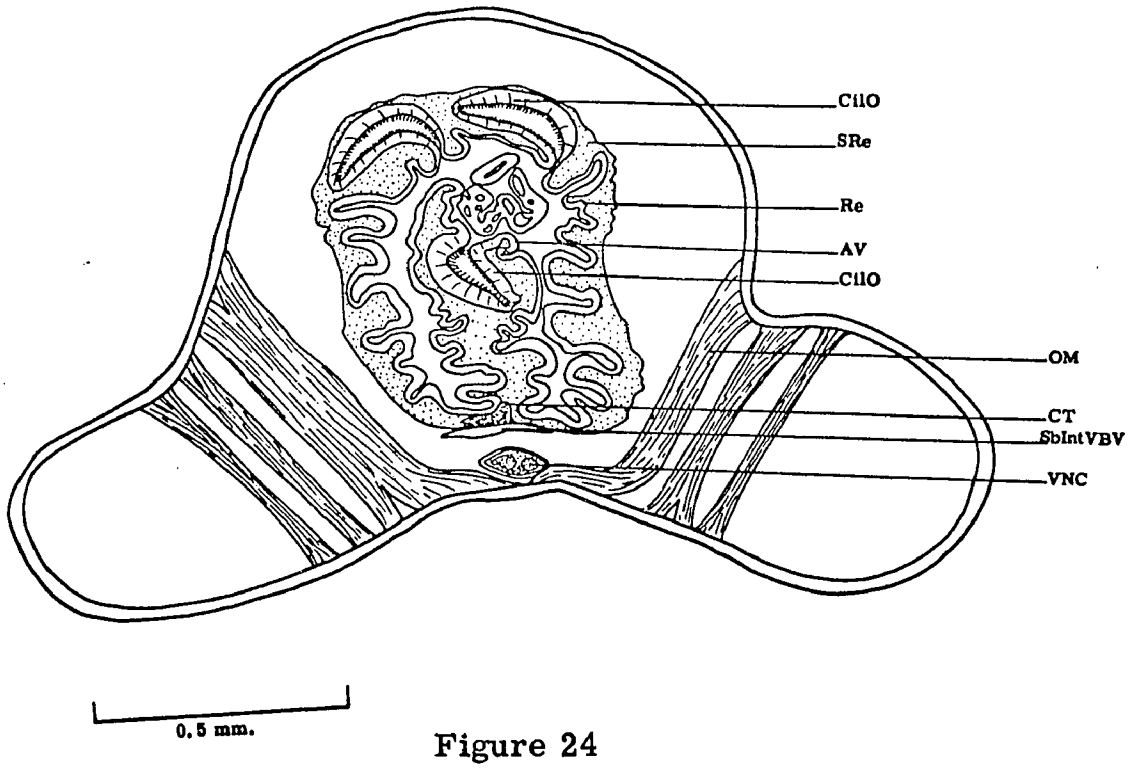


Figure 24

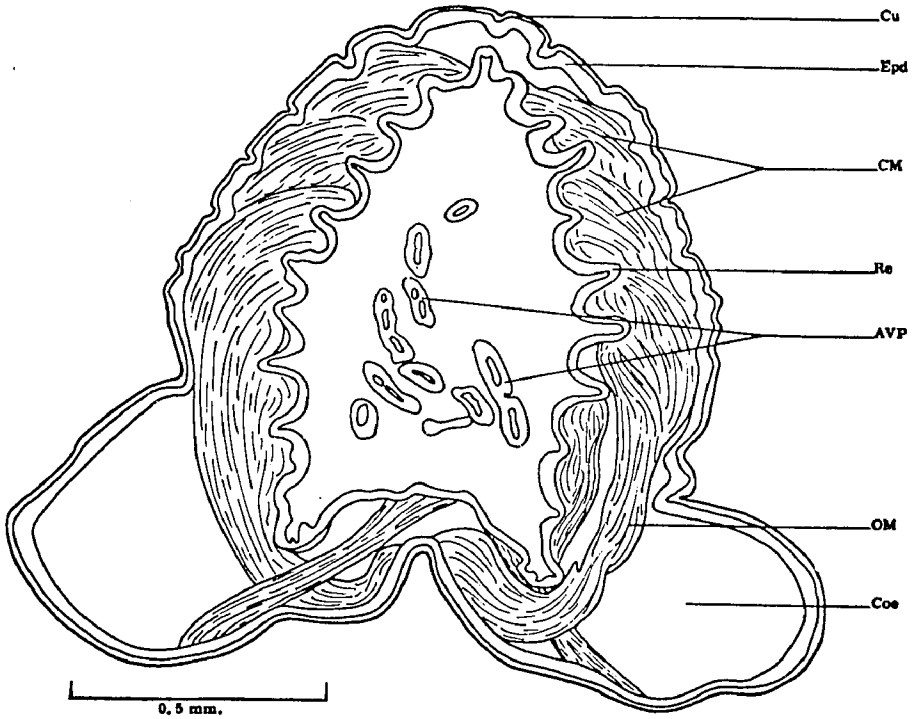


Figure 25

Figure 26. Cross section of branchia. Gomori's trichrome stain, 190X.


Figure 26

Figure 27. Sagittal section of branchia. Branchial capillaries within epidermal grooves, Gomori's trichrome stain, 620X.

Figure 28. Sagittal section of branchia. Connection of branchial capillaries with branchial vessels. Gomori's trichrome stain, 645X.


Figure 27

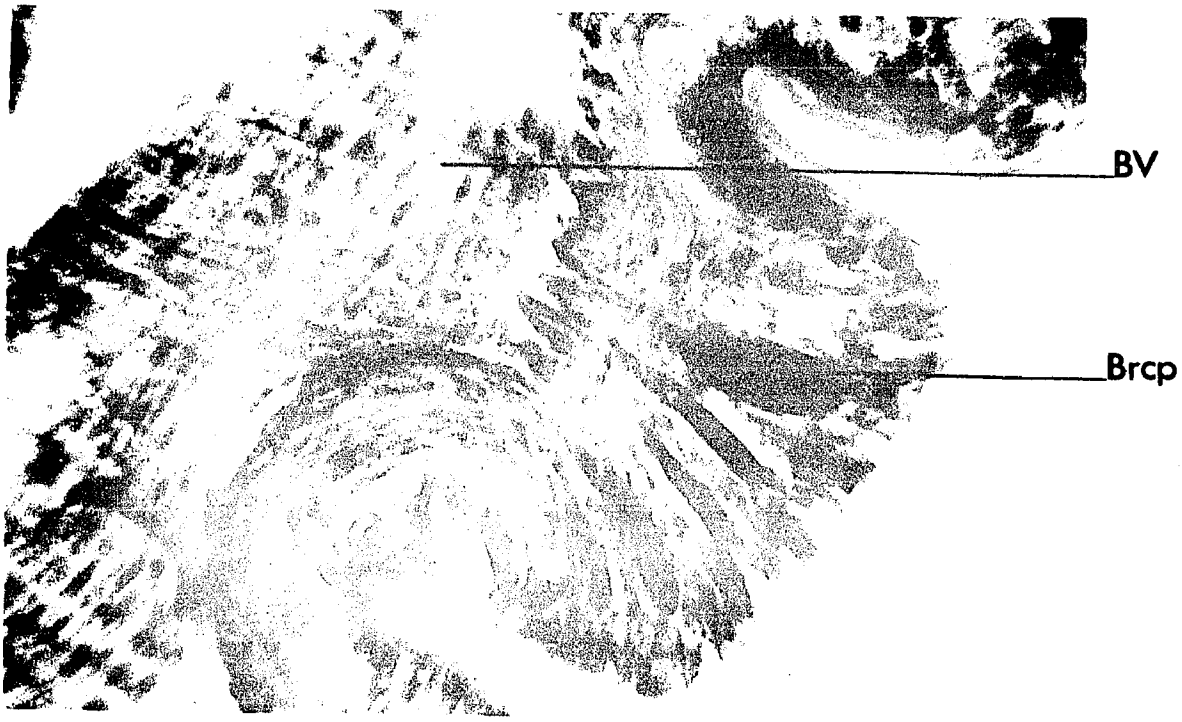


Figure 28

Figure 29. Sagittal section of heart body. Gomori's trichrome stain, 1140X.

Figure 30. Sagittal section at junction of stomach and intestine. Heart body connected to dorsal wall of intestine by a sheet of connective tissue. Gomori's trichrome stain, 150X.

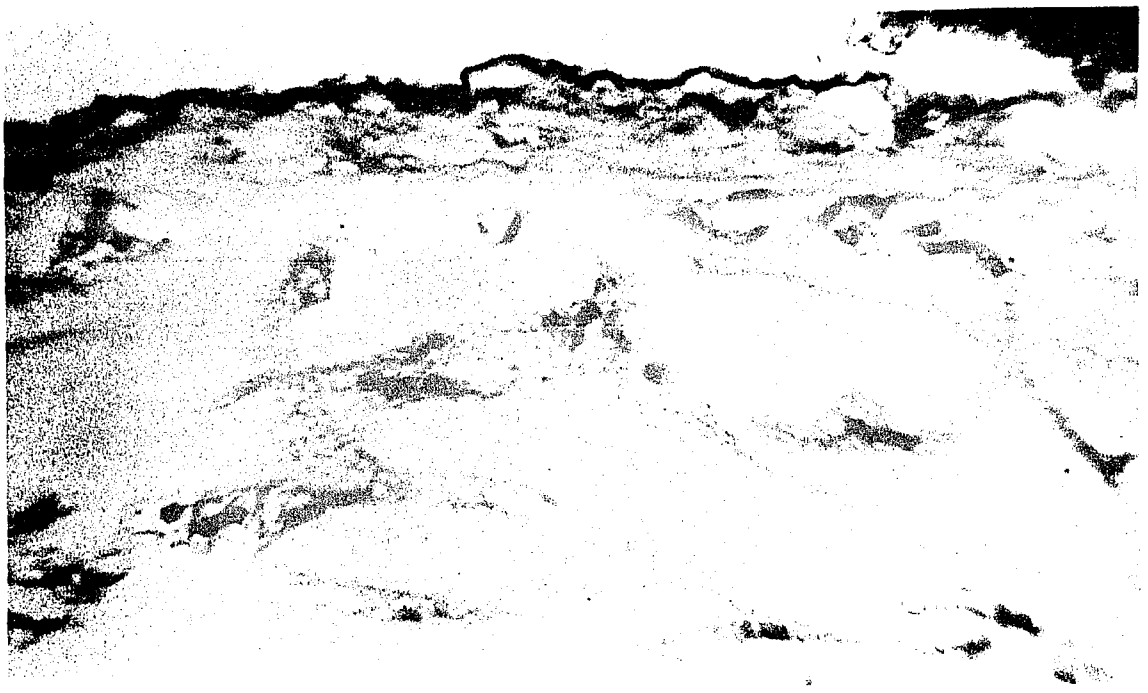

Figure 29

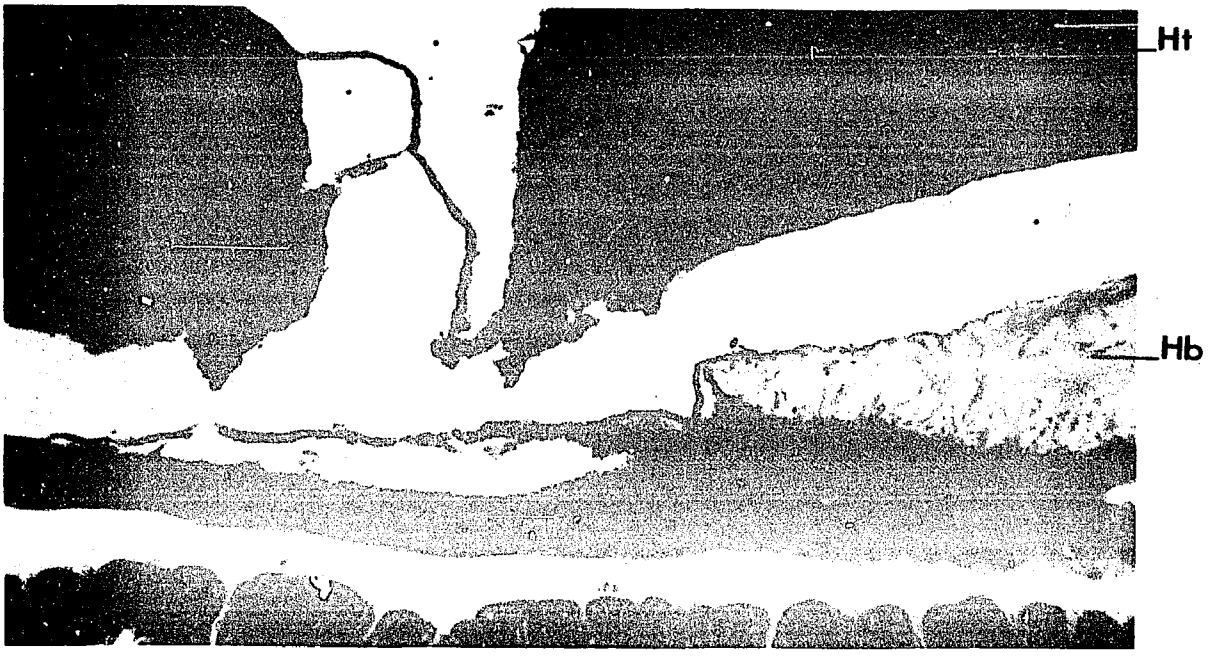


Figure 30

Figure 31. Cross section through glandular ridge. (setigerous segment nine).

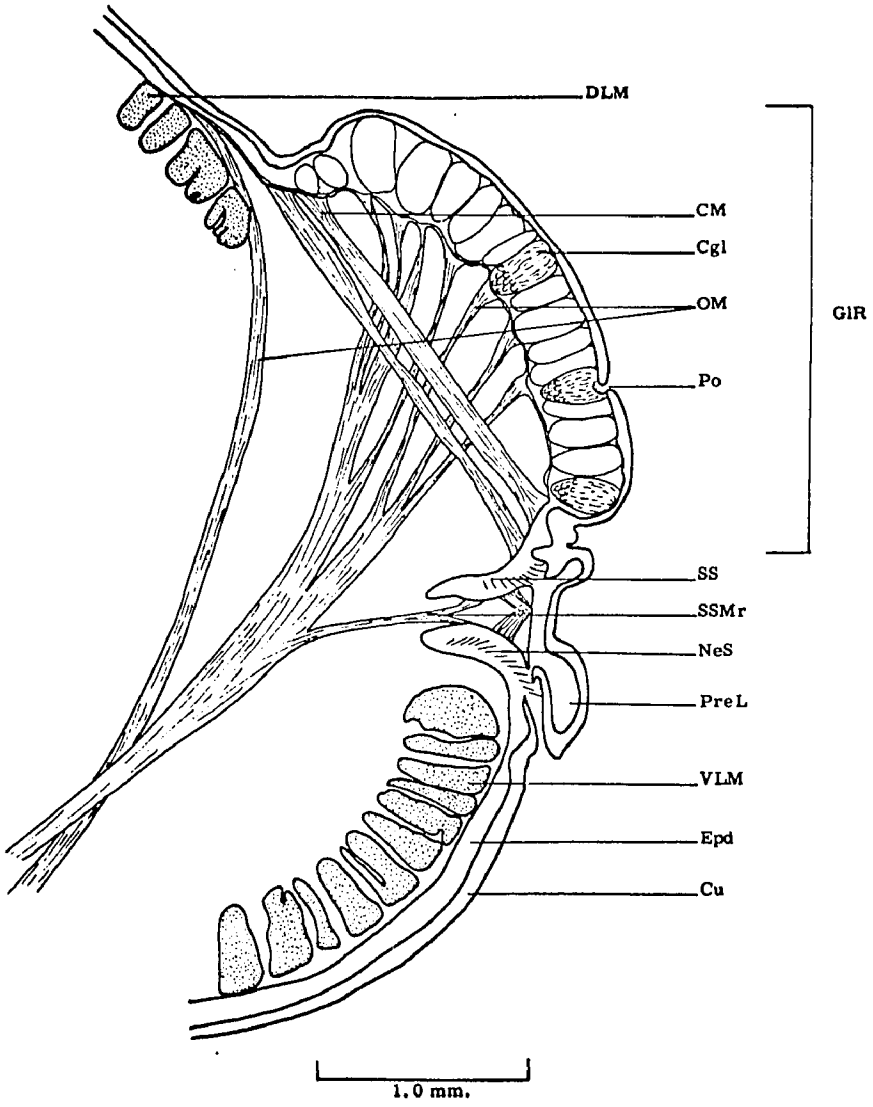


Figure 31

Figure 32. Setal sac and setal sac muscles in prebranchial region. Only that part of the setal sac which projects into the coelom is drawn. 250X.

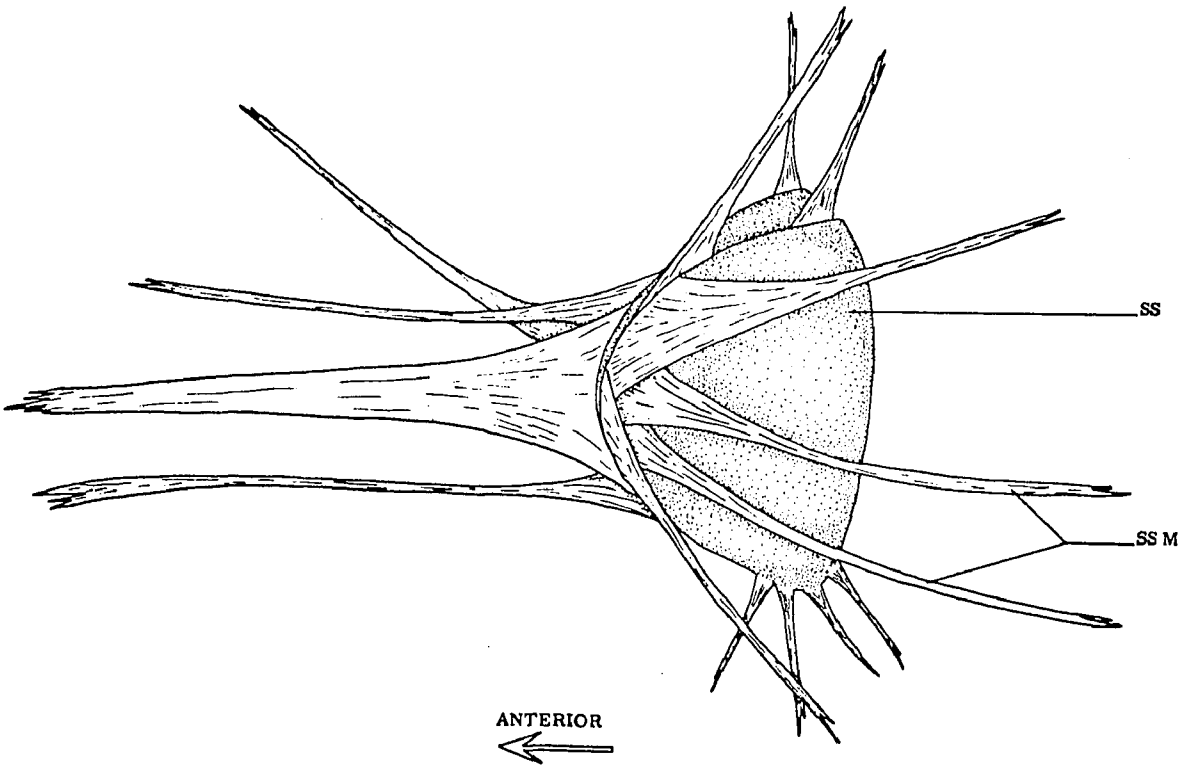


Figure 32

Figure 33. Cross section of setal sac and lateral organ of setigerous segment one.

Figure 34. Sagittal section of setal sac and setal sac muscles located in the lateral ridge (branchial region).

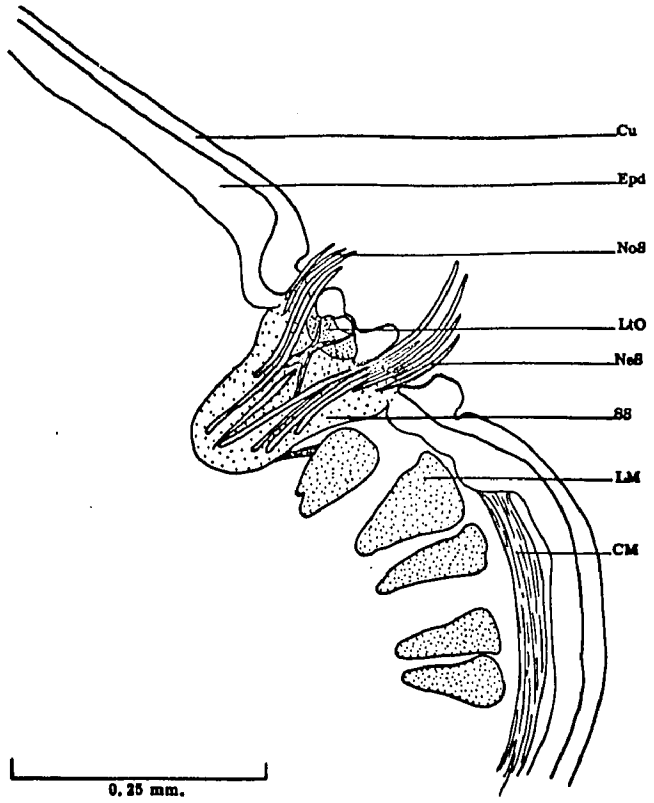


Figure 33

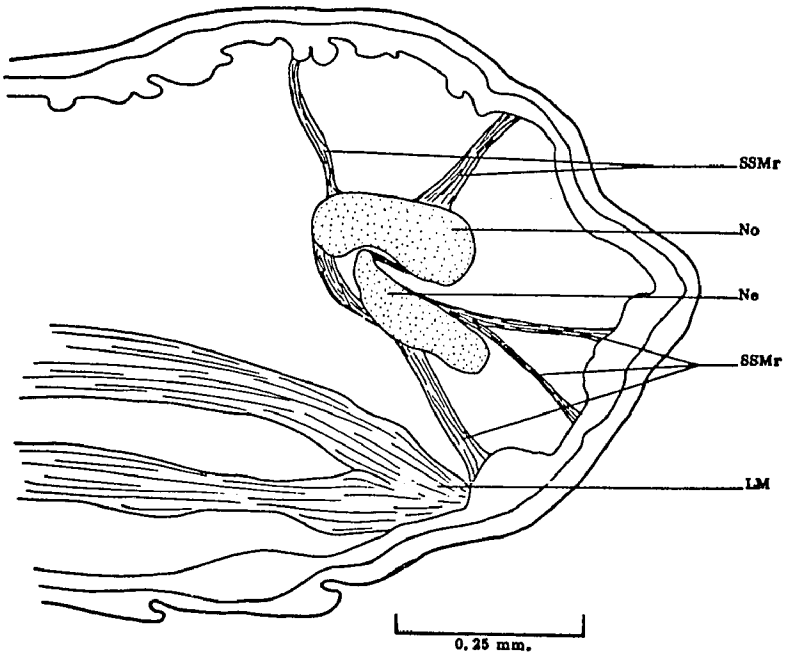


Figure 34

Figure 35. Diagram of the relationship between the inverted proboscis, proboscis retractor muscles, and injector organ septa.

Figure 36. Diagram of the muscular suspensory ligaments of the alimentary tract, 4.5X.

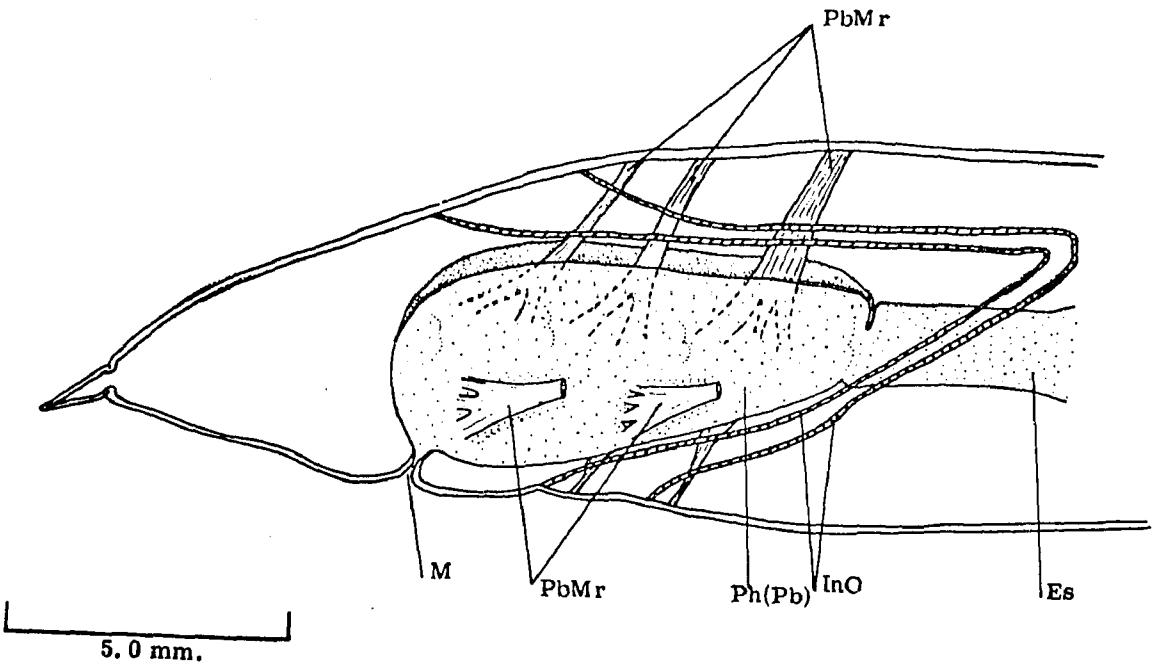


Figure 35

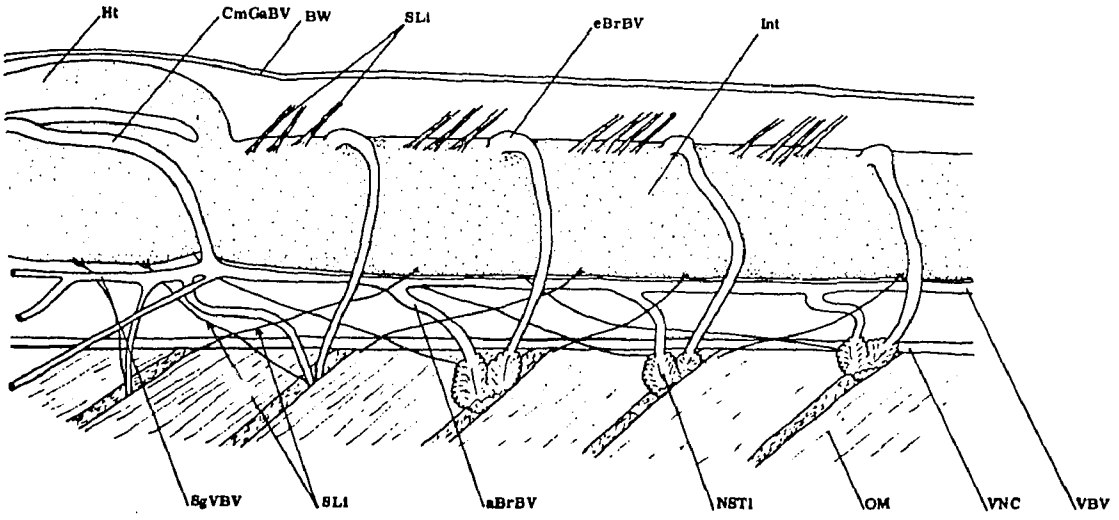


Figure 36

Figure 37. Sagittal section of the dorsal body wall at the junction of the prebranchial and branchial regions. Circular muscle layer reduced. Gomori's trichrome stain, 115X.

Figure 38. Sagittal section of ventral body wall at the junction of the prebranchial and branchial regions. Oblique muscles increase in number and thickness in this region. Gomori's trichrome stain, 50X.

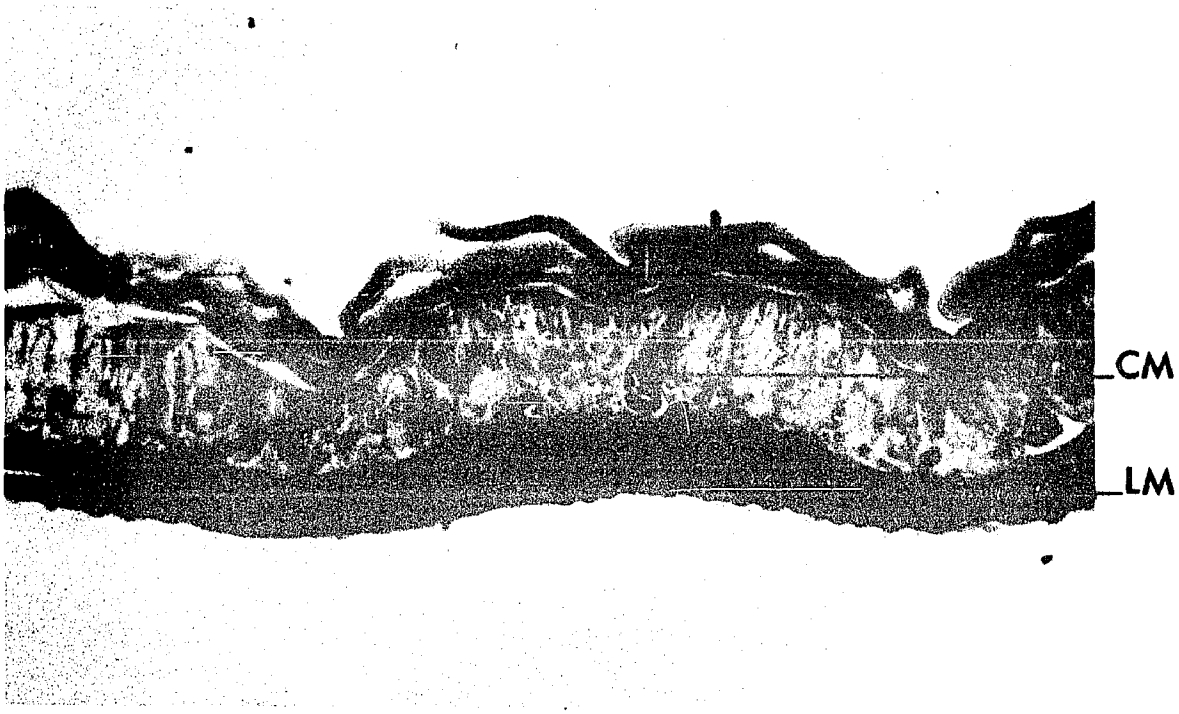


Figure 37


Figure 38

Figure 39. Sagittal section of dorsal body wall in the prebranchial region, P.A.S.,245X.

Figure 40. Sagittal section through the mouth 65X.

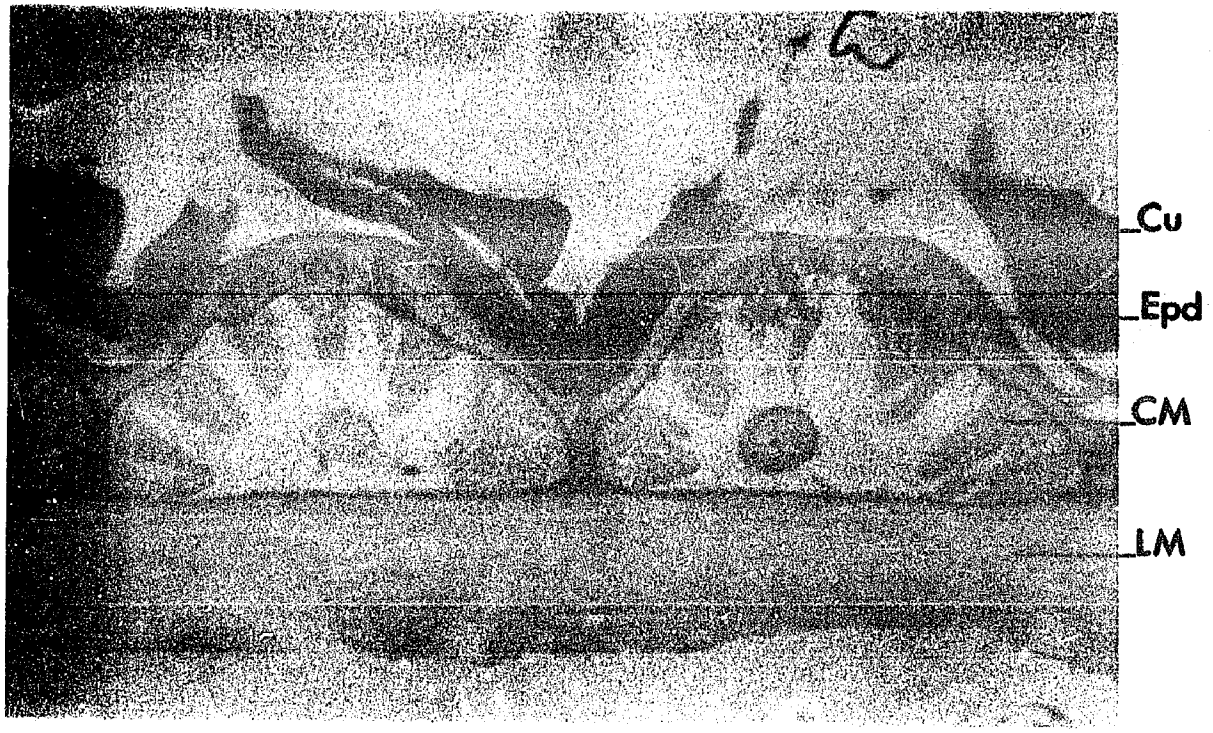


Figure 39

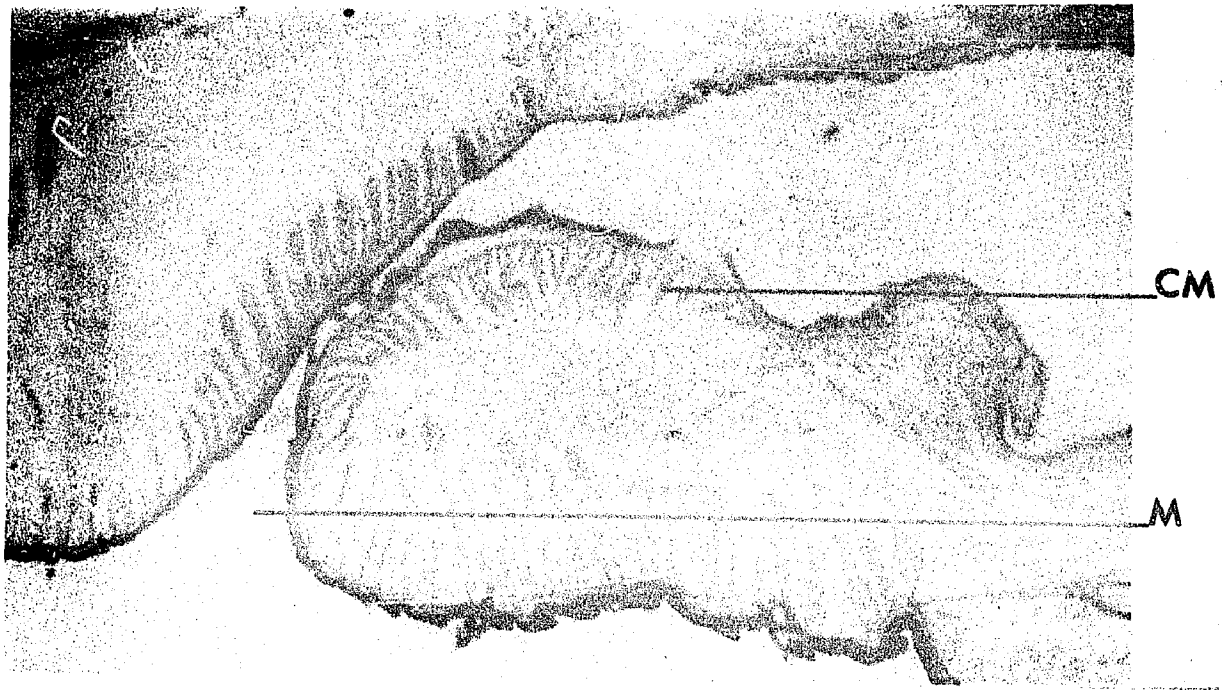


Figure 40

Figure 41. Detail of septum in the postbranchial region. Gomori's trichrome stain, 700X.

Figure 42. Sagittal section of postbranchial region. Gomori's trichrome stain, 30X.

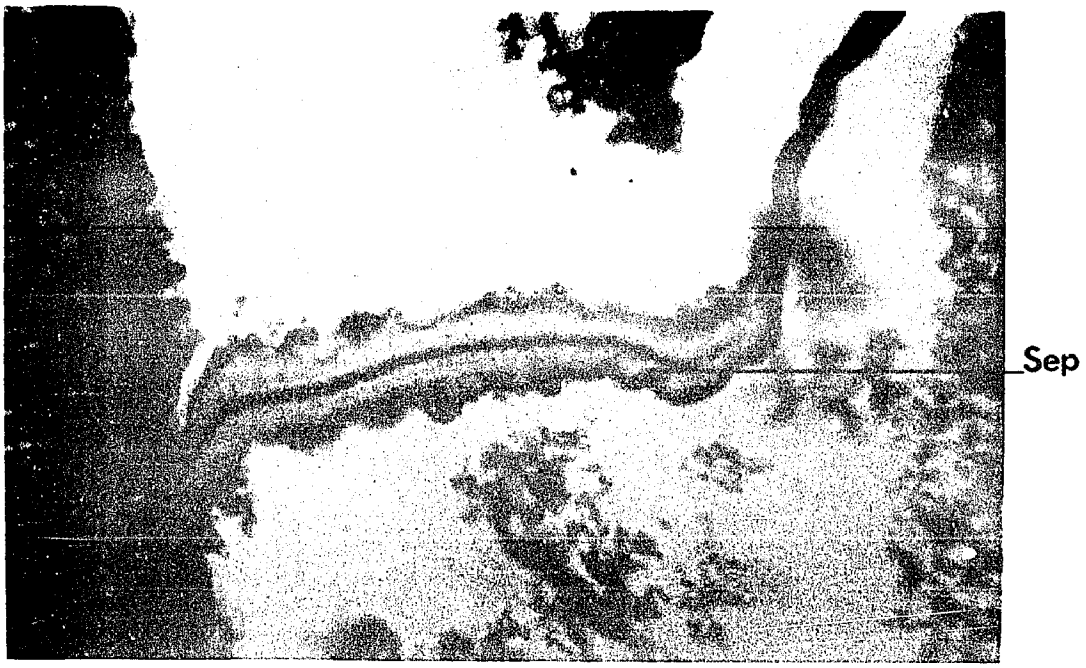


Figure 41

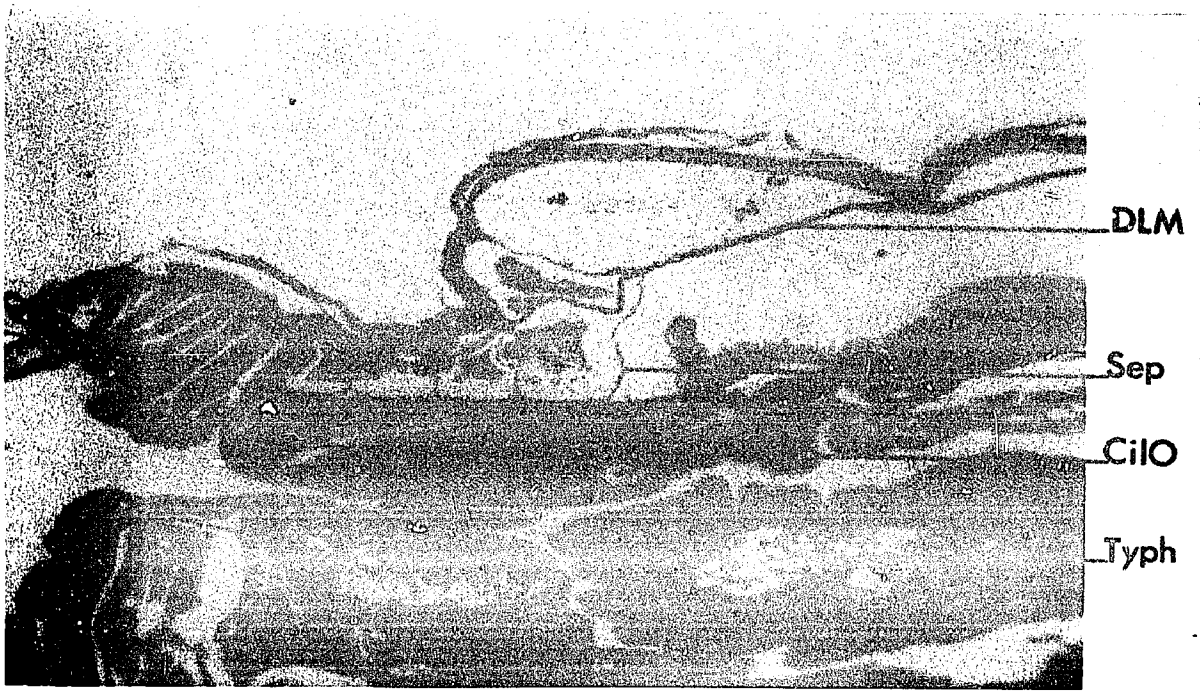


Figure 42

Figure 43. Diagram of an anterior nephridium and its relationship to the segmental blood vessels, 60X.

Figure 44. Diagram of a posterior nephridium and its relationship to the segmental blood vessels, 60X.

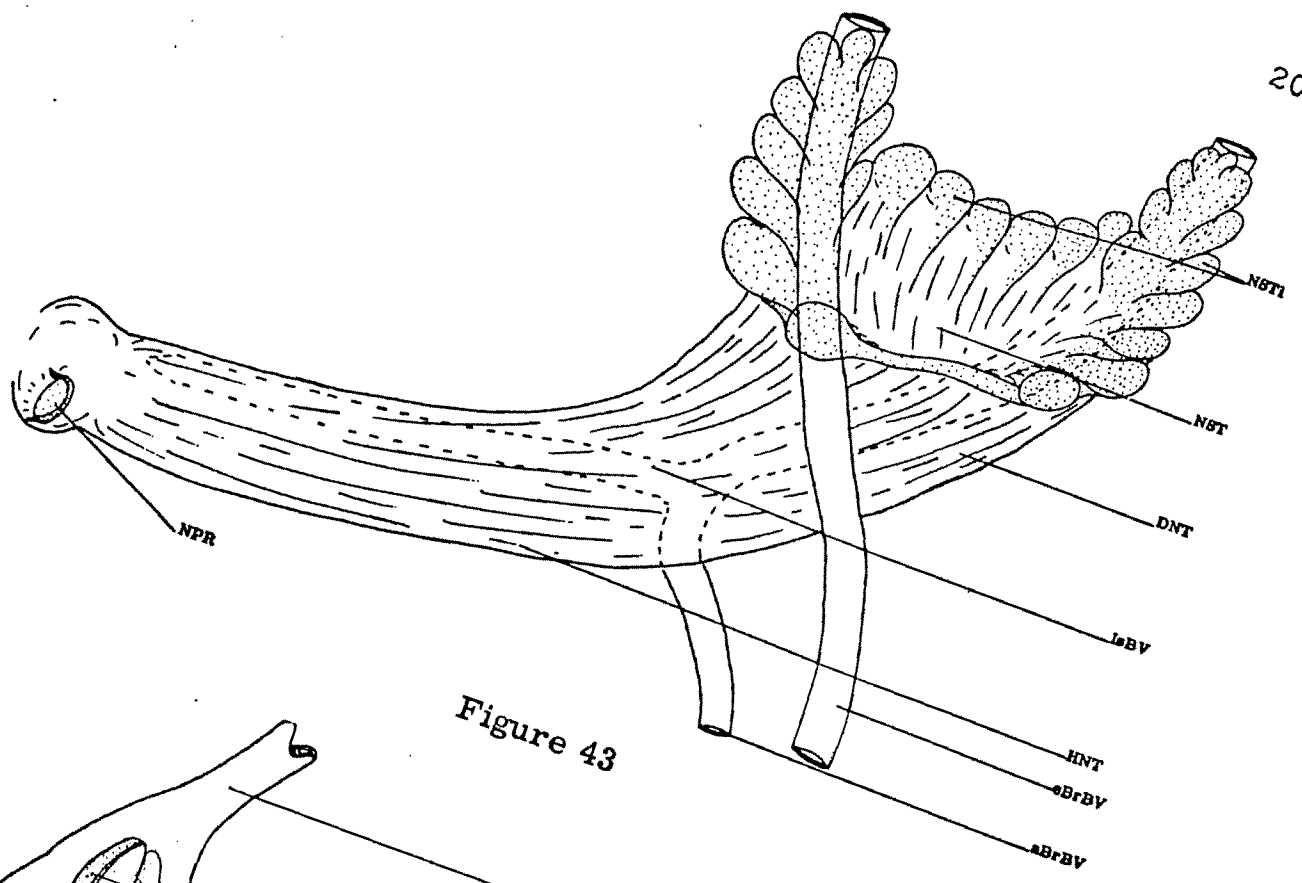


Figure 43

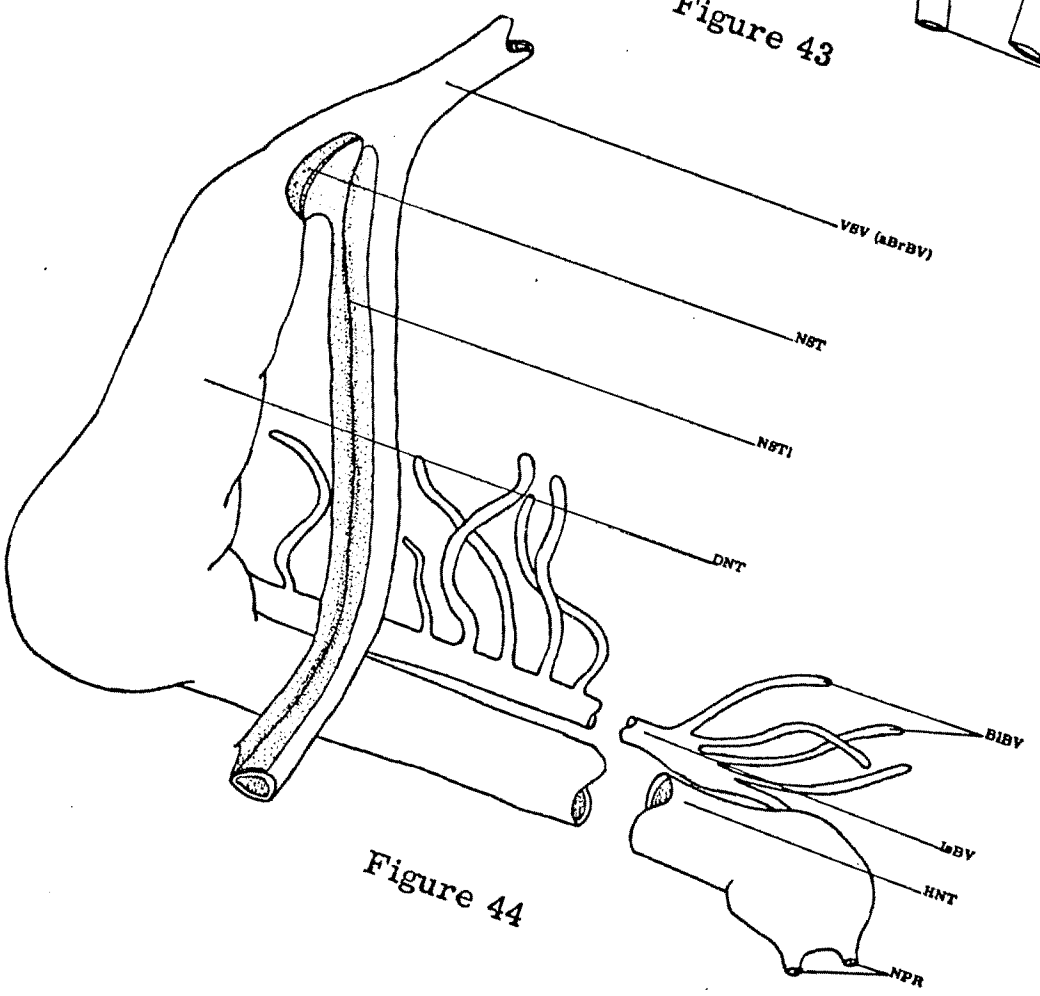


Figure 44

Figure 45. Cross section of dorsal body wall. Note: epidermal support cells. Hematoxylin and Eosin, 785X.

Figure 46. Types A and B gland cells near glandular ridge of setigerous segment nine. Cross section. Hematoxylin and Eosin, 615X.

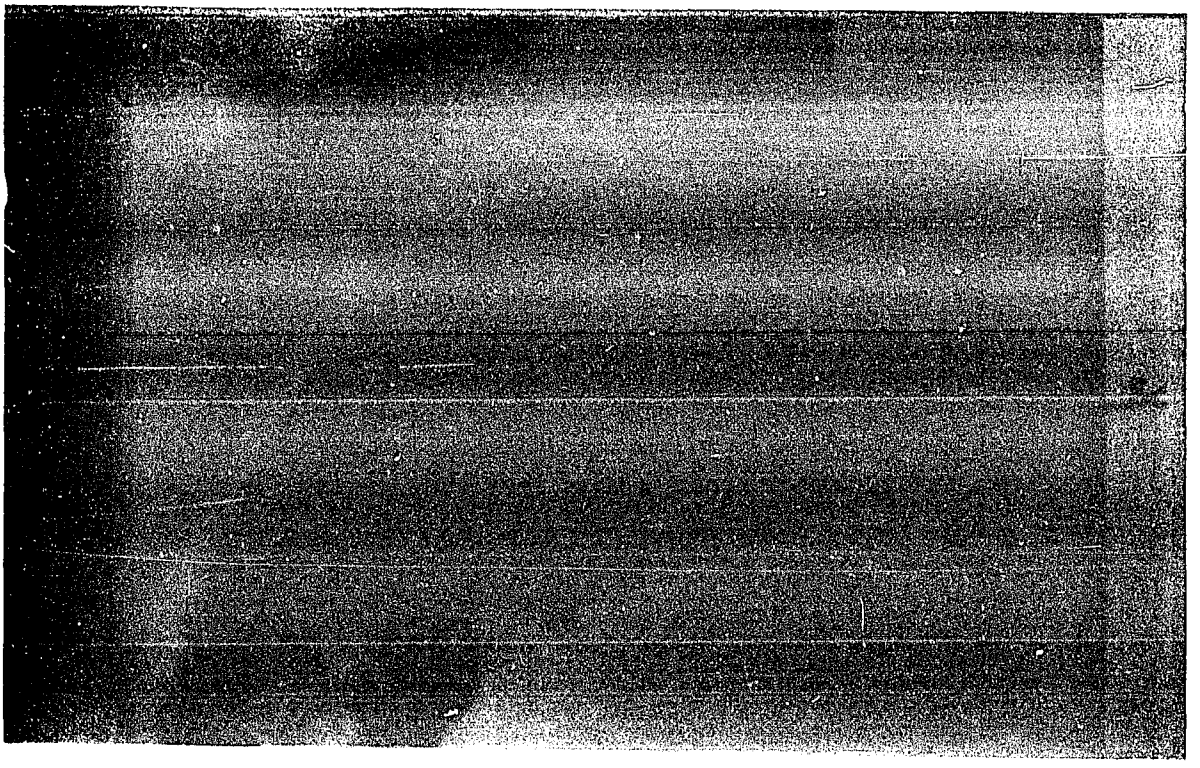

Figure 45

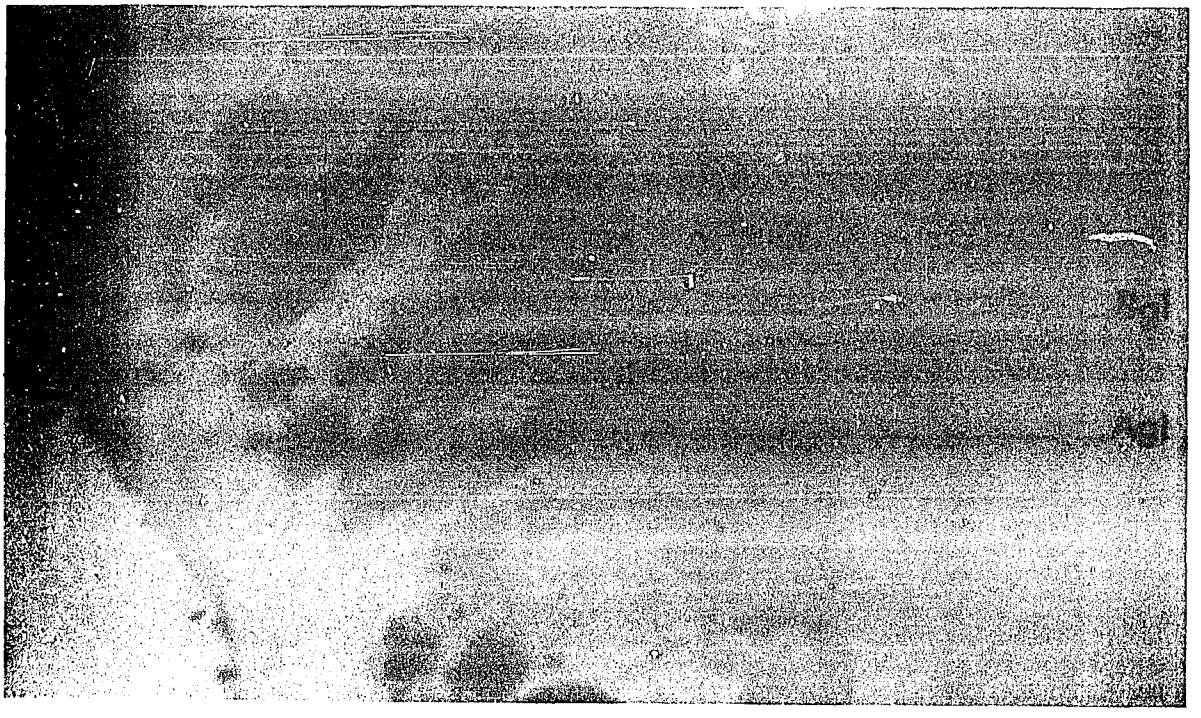

Figure 46

Figure 47. Cross section of dorsal body wall at junction of postbranchial segments one and two. Numerous type A gland cells with one pore opening to the outside. Hematoxylin and Eosin, 615X.

Figure 48. Cross section of glandular ridge at setigerous segment nine. Hematoxylin and Eosin, 620X.


Figure 47

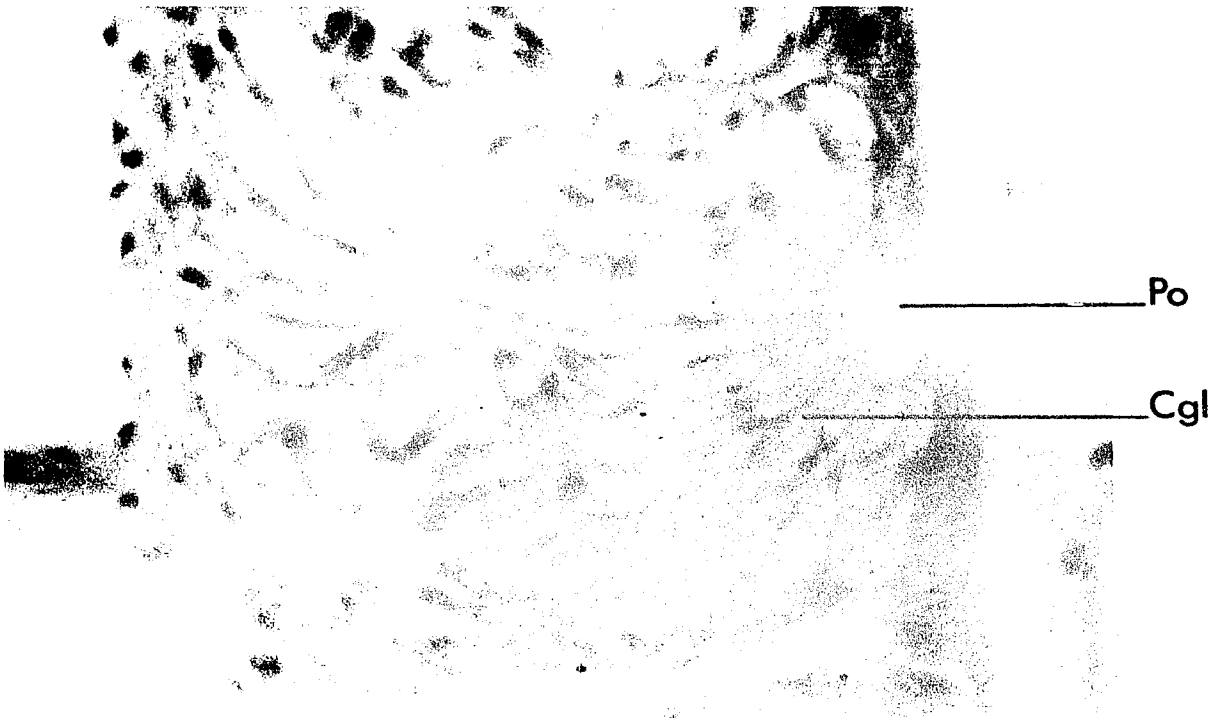


Figure 48

Figure 49. Tangential section of lateral body wall. Close association of type A and type C gland cells. Numerous gland cells share a single pore. Hematoxylin and Eosin, 680X.


Figure 49

Figure 50. Sagittal section of dorsal body wall. Detail of cuticular invagination which anchors the cuticle to the epidermis. P.A.S. 790X.

Figure 51. Sagittal section of ventral body wall. Detail of the attachment of oblique muscle bands to cuticular invaginations Gomori's trichrome stain, 570X.

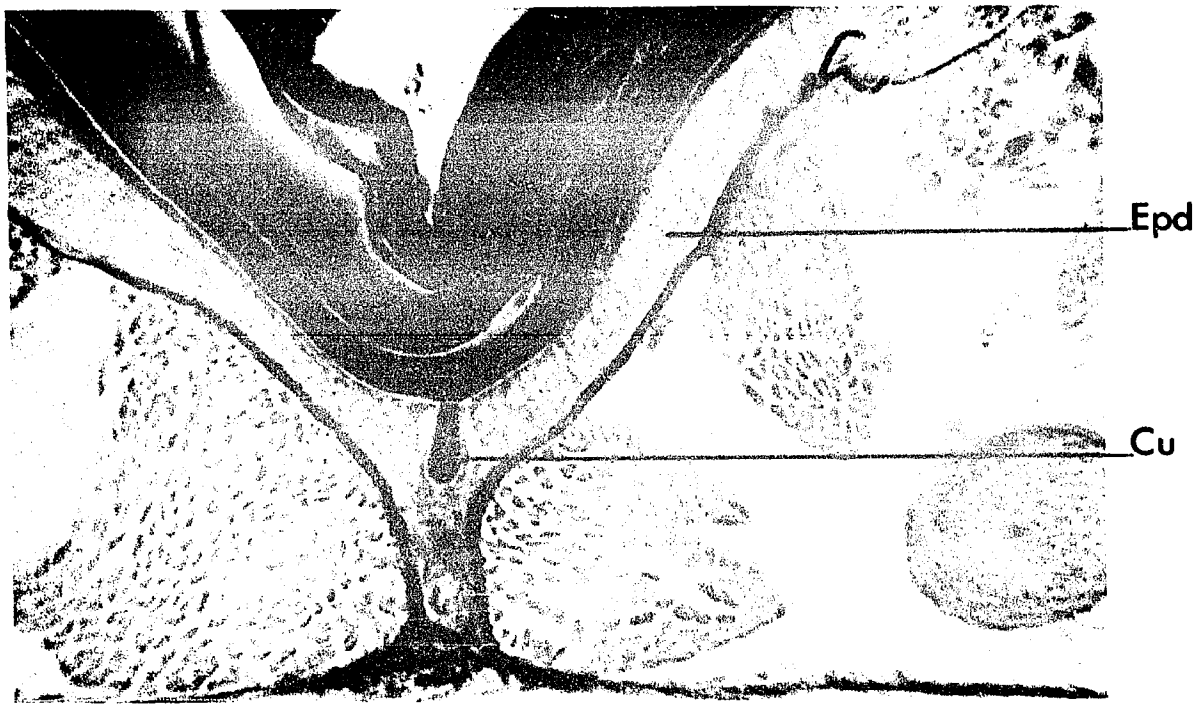


Figure 50

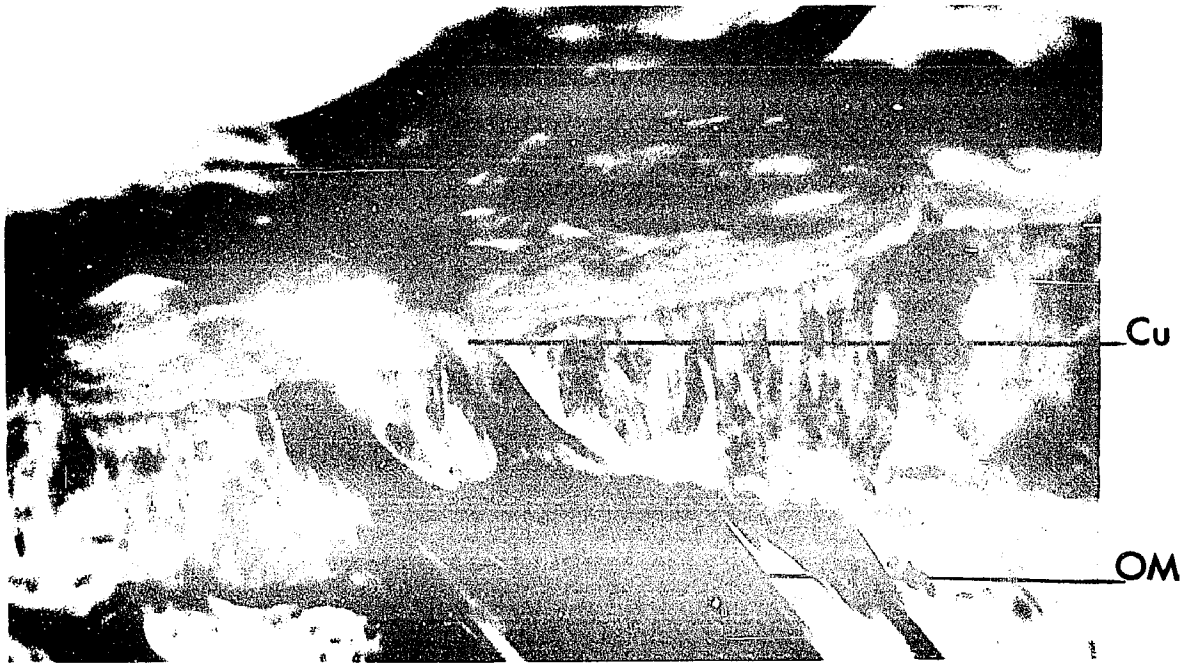


Figure 51

Figure 52. Cross section of lateral organ and lateral organ retractor muscles. Branchial region.

Figure 53. Sagittal section of lateral organ and extension of lateral organ into postsetal lobe. Branchial region.

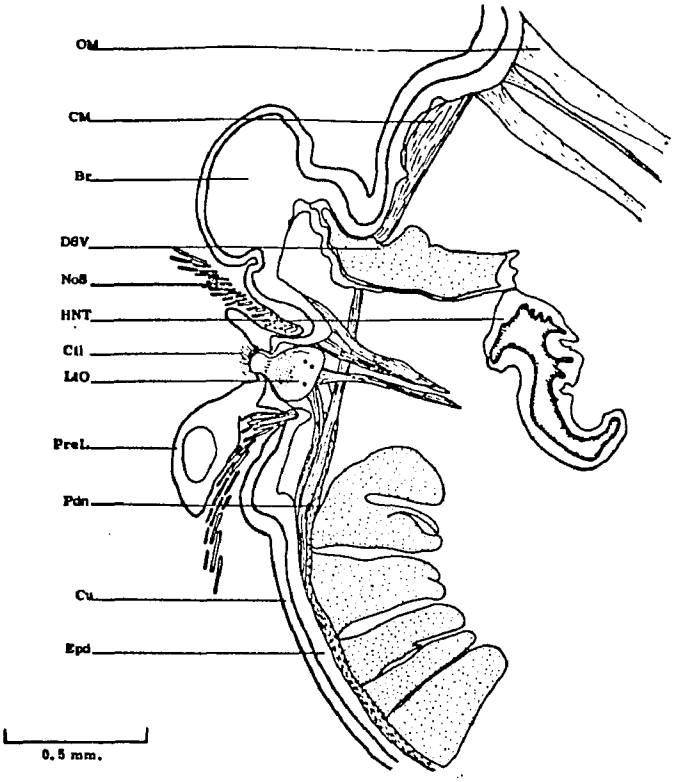


Figure 52

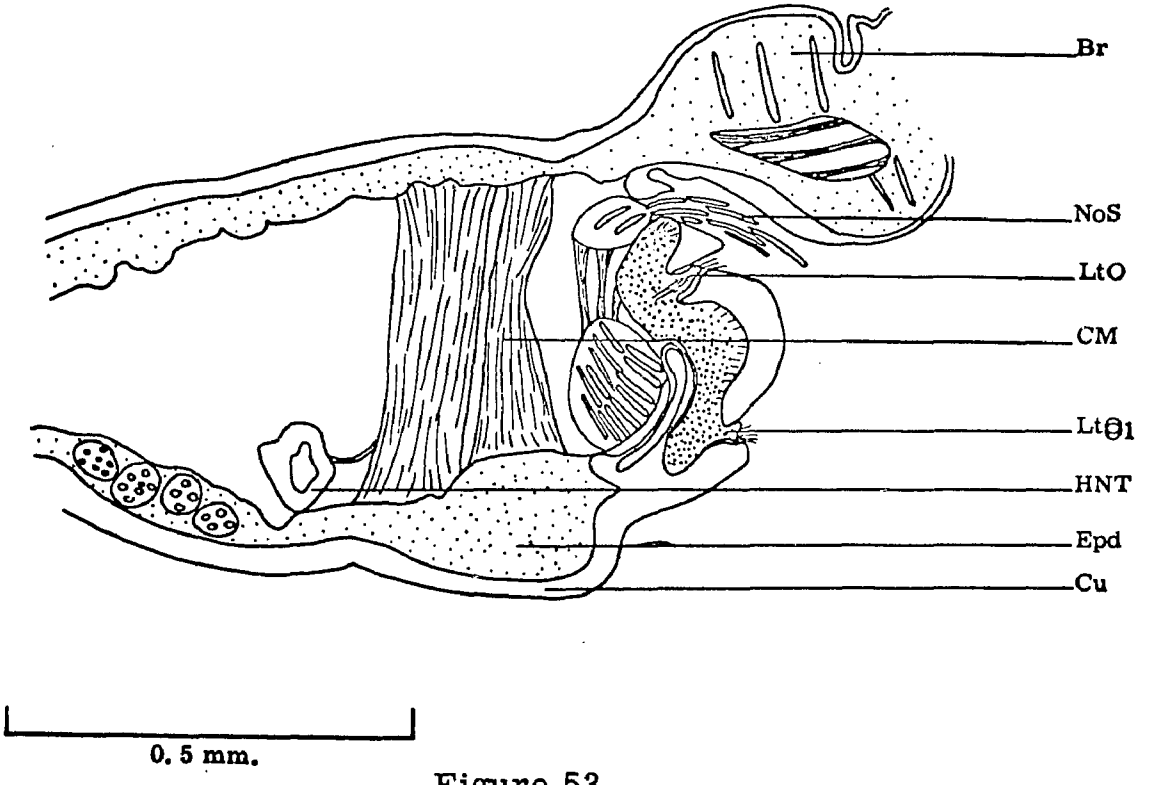


Figure 53

Figure 54. Cross section of lateral body wall in the branchial region. Detail of the branchial fenestrations. Gomori's trichrome stain, 875X.

Figure 55. Detail of eye embedded in the brain. The eye is composed of unstained, brown-colored granules. P.A.S., 1215X.

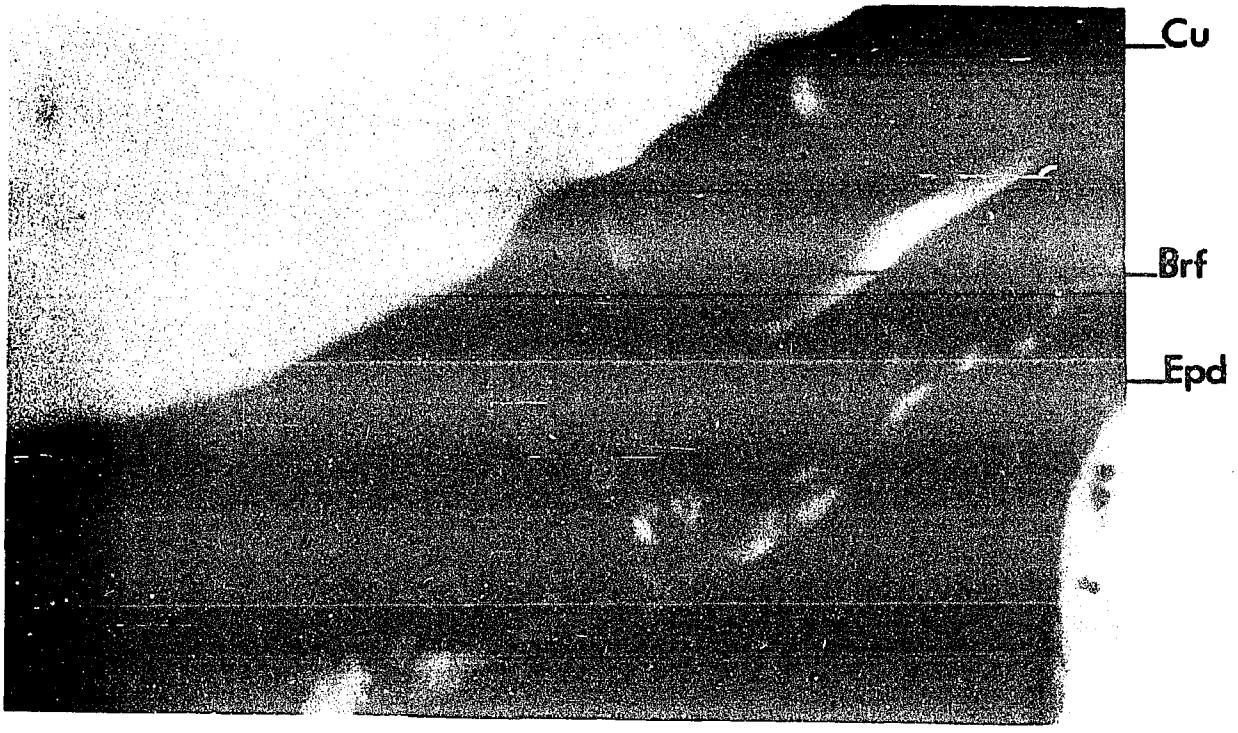


Figure 54

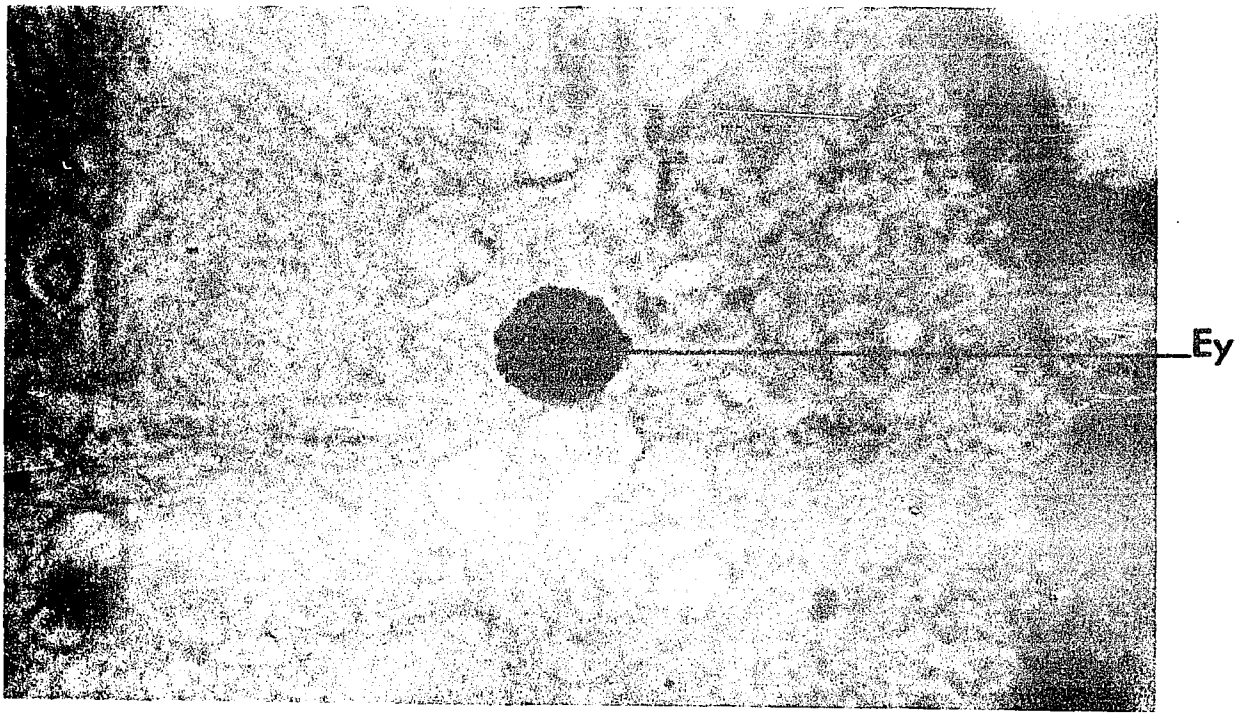


Figure 55

Figure 56. Detail of buccal epithelium. Gomori's trichrome stain, 820X.

Figure 57. Cross section of prebranchial region showing the pattern of folds in the pharynx. Gomori's trichrome stain, 30X.


Figure 56

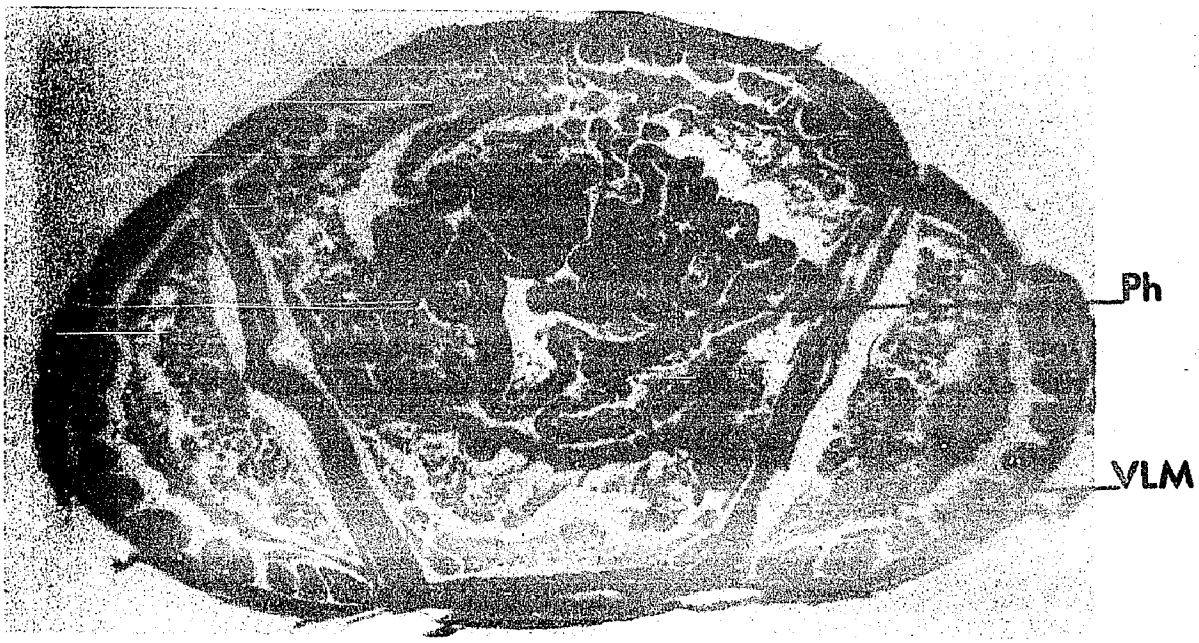


Figure 57

Figure 58. Ciliated, columnar epithelium of the pharynx. Gomori's trichrome stain, 780X.

Figure 59. Ciliated columnar epithelium of the esophagus. Gomori's trichrome stain, 715X.

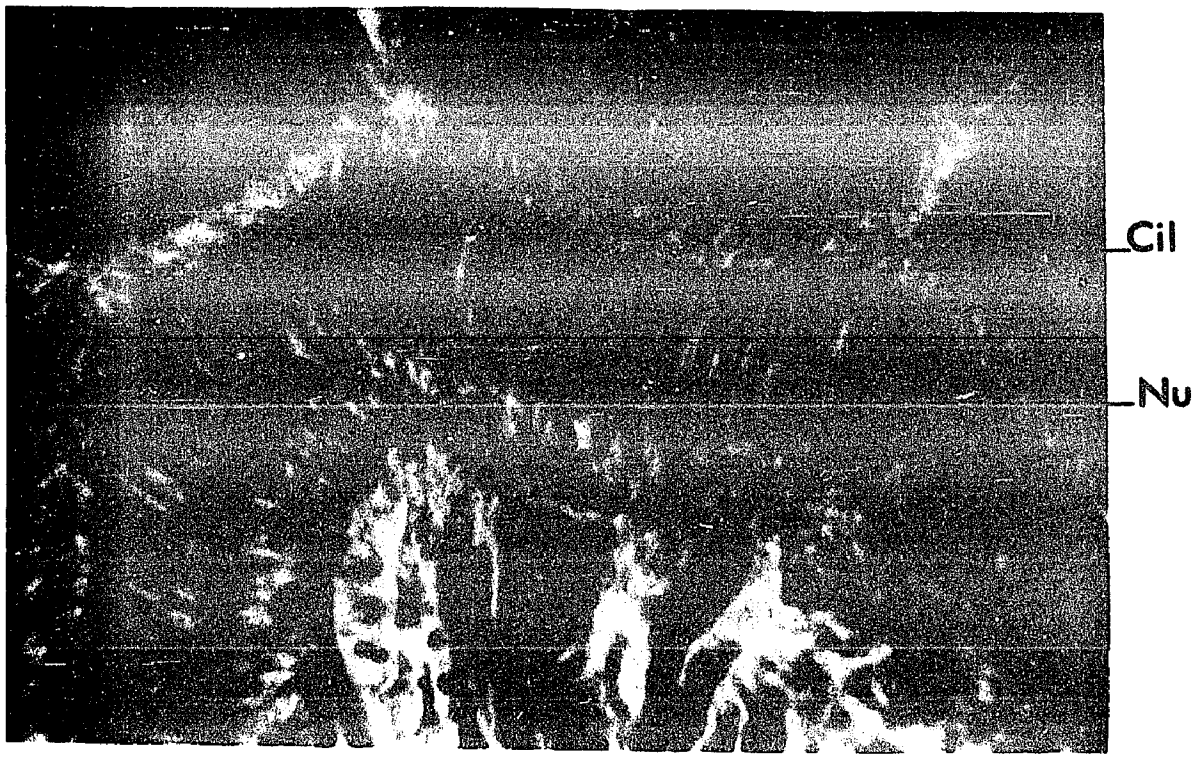


Figure 58

Figure 59

Figure 60. Epithelium of the dorsal wall of the middle part of the stomach. Sagittal section. Gomori's trichrome stain, 620X.

Figure 61. Epithelium of the dorsal wall of the posterior part of the stomach. Sagittal section. Gomori's trichrome stain, 570X.

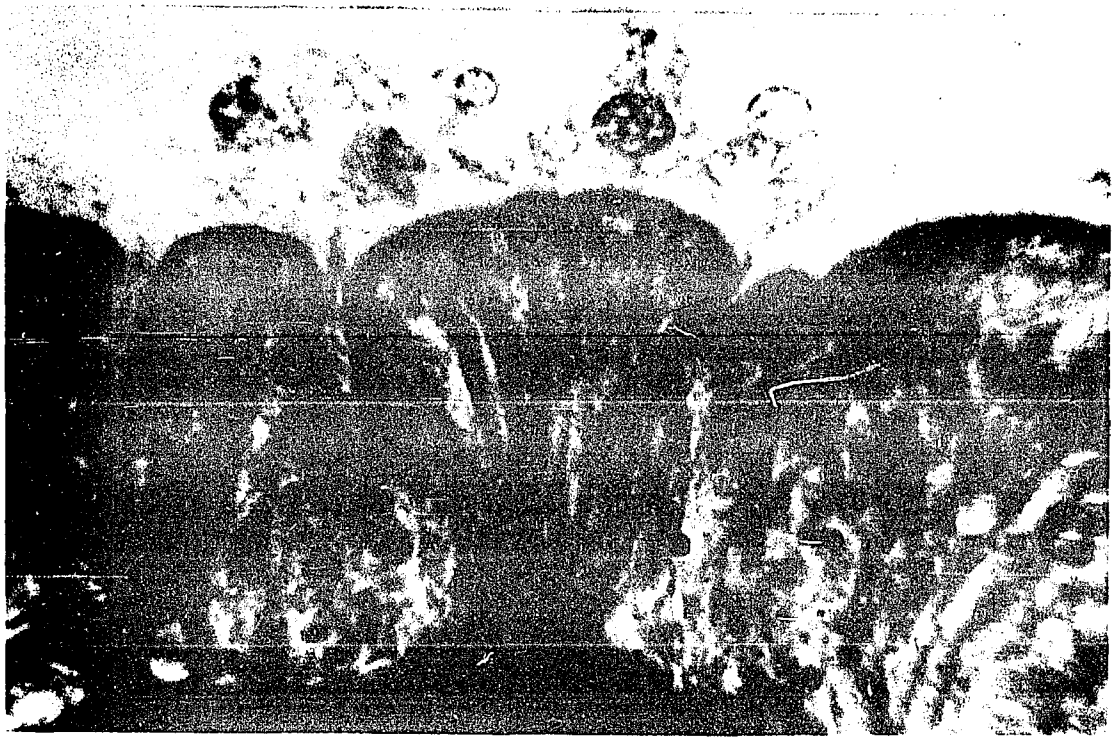

Figure 60


Figure 61

Figure 62. Epithelium of the anterior part of the intestine. Sagittal section. Gomori's trichrome stain, 820X.

Figure 63. Epithelium of the dorsal wall of the typhlosole in the anterior part of the intestine. Sagittal section. Gomori's trichrome stain, 735X.

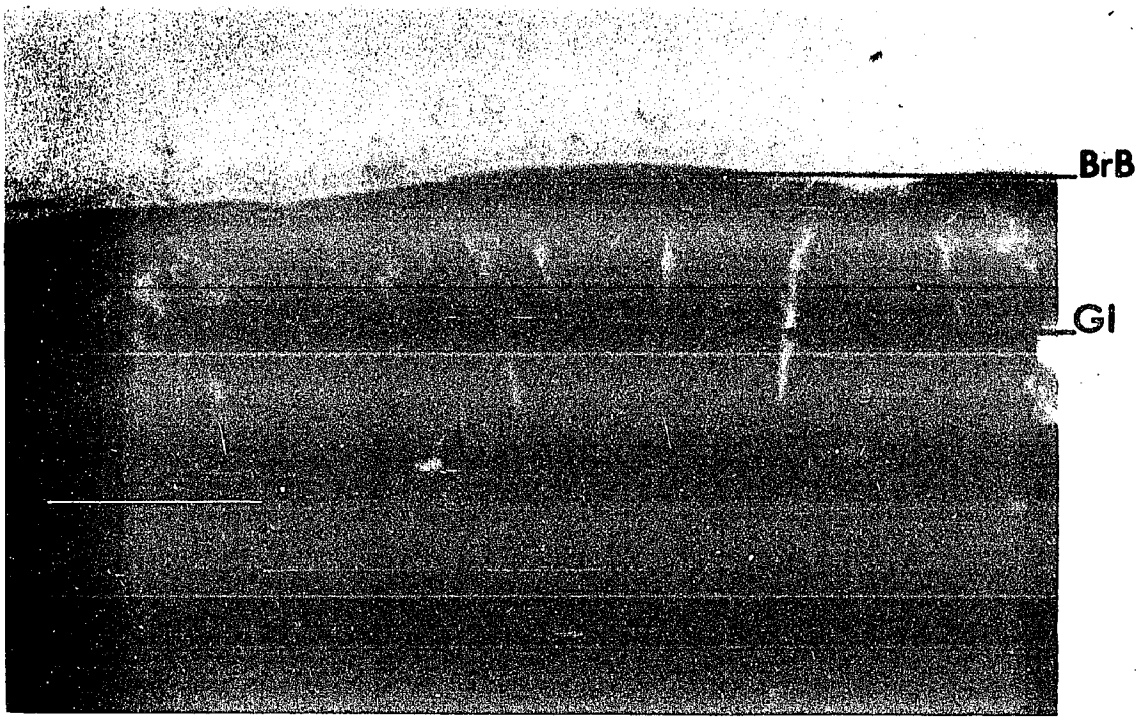


Figure 62

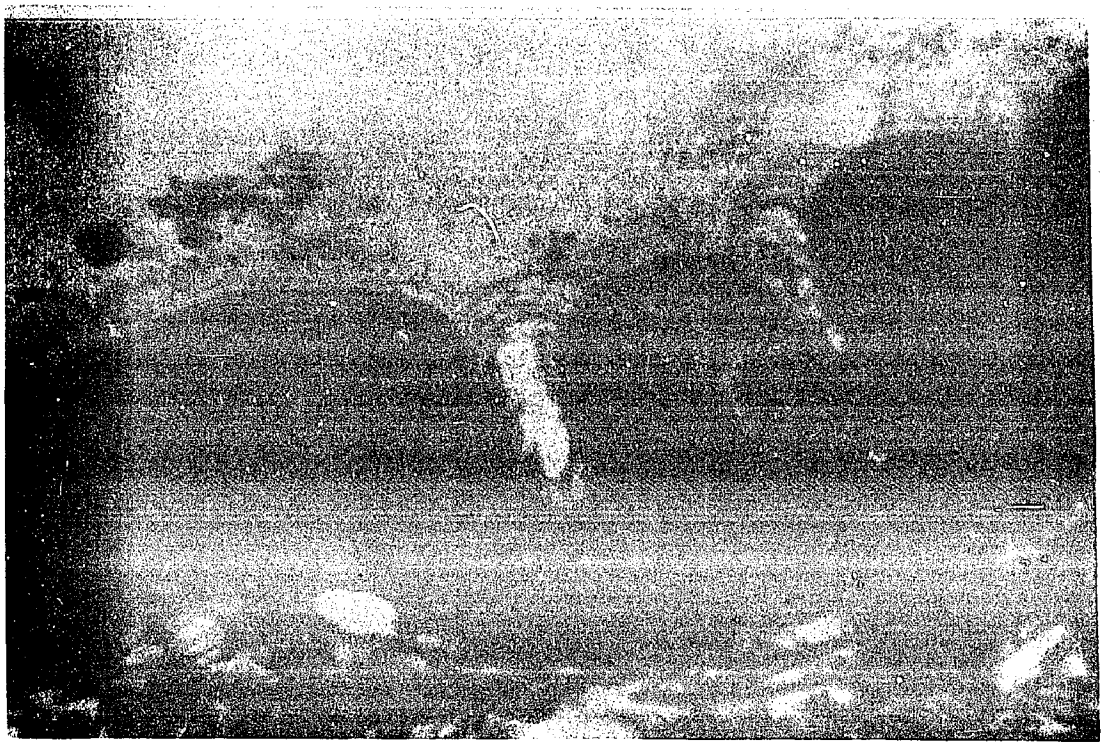

Figure 63

Figure 64. Epithelium of dorsal wall of anterior part of stomach. Sagittal section. Hematoxylin and Eosin, 770X.

Figure 65. Epithelium of dorsal wall of intestine. Sagittal section in region of setigerous segment 18. Hematoxylin and Eosin, 870X.

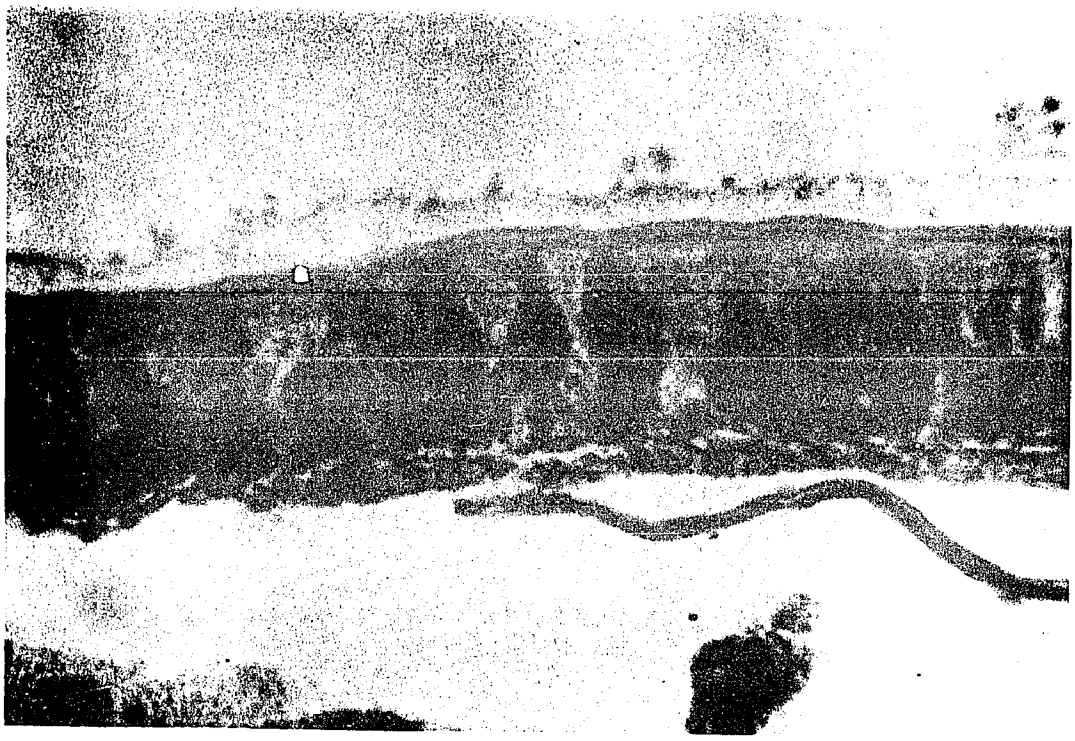

Figure 64

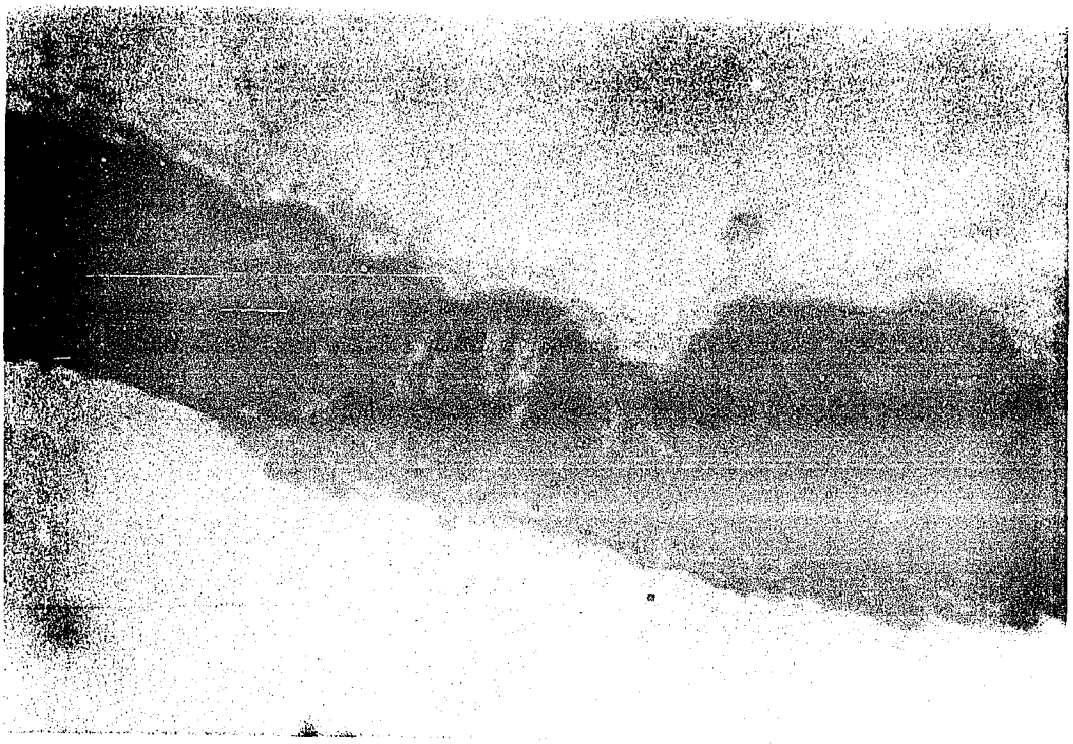

Figure 65

Figure 66. Ciliated columnar epithelium of the rectal ciliated organ. Sagittal section. Hematoxylin and Eosin, 1000X.

Figure 67. Non-ciliated epithelium of posterior part of rectum (near anal papillae) Hematoxylin and Eosin, 910X.

Figure 66

Figure 67

Figure 68. Ventral ciliated groove of the intestine. Cross section. Gomori's trichrome stain, 440X.

Figure 69. Chloragogen cells of the outer wall of the intestinal sinus. Gomori's trichrome stain, 650X.

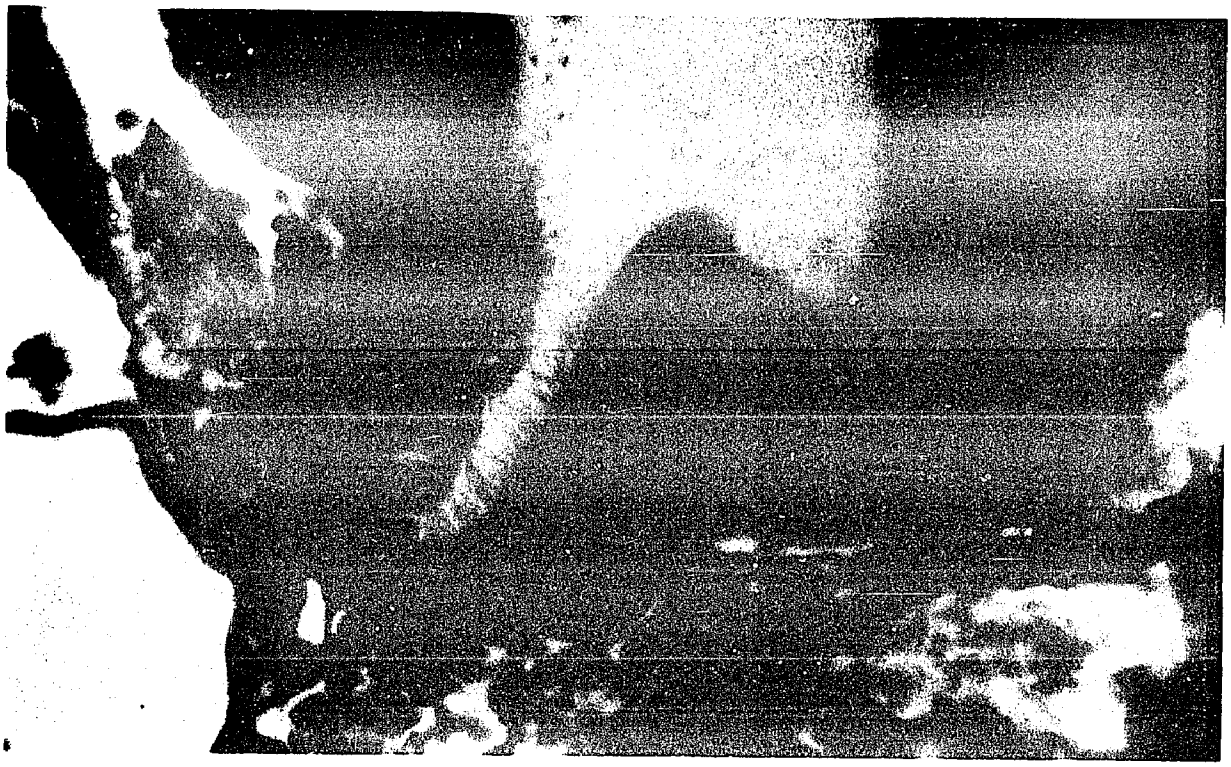

Figure 68

Figure 69

Figure 70. Cross section of the subpharyngeal ganglion. Gomori's trichrome stain, 520X.

Figure 71. Sagittal section of the brain. Detail of the occipital horns. P.A.S., 1140X.

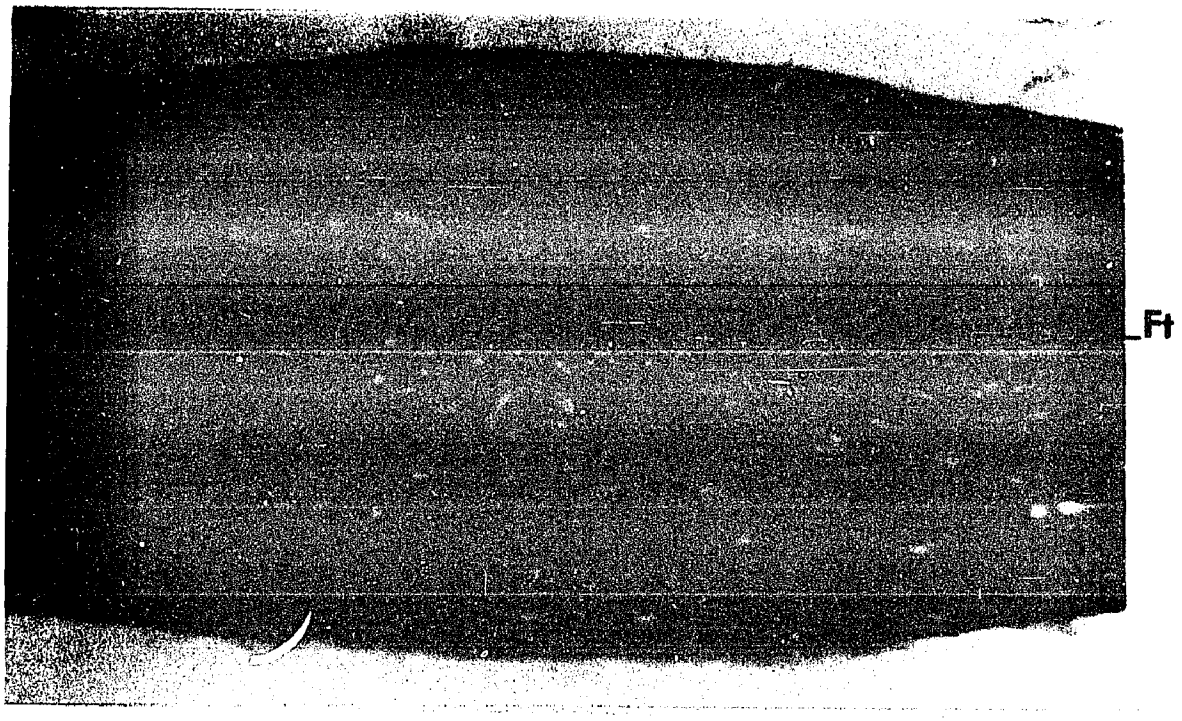


Figure 70


Figure 71

Figure 72. Cross section of palpode.

Figure 73. Cross section at junction of palpode and annulated part of prostomium. Detail of anterior part of brain.

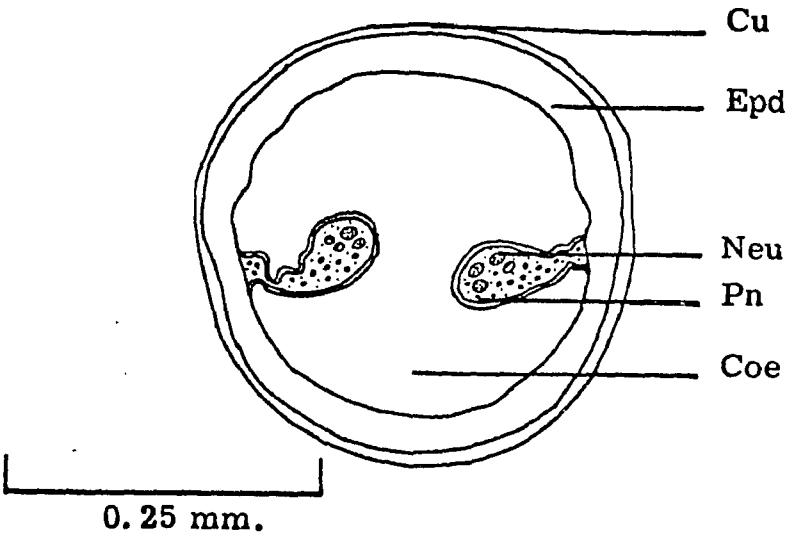


Figure 72

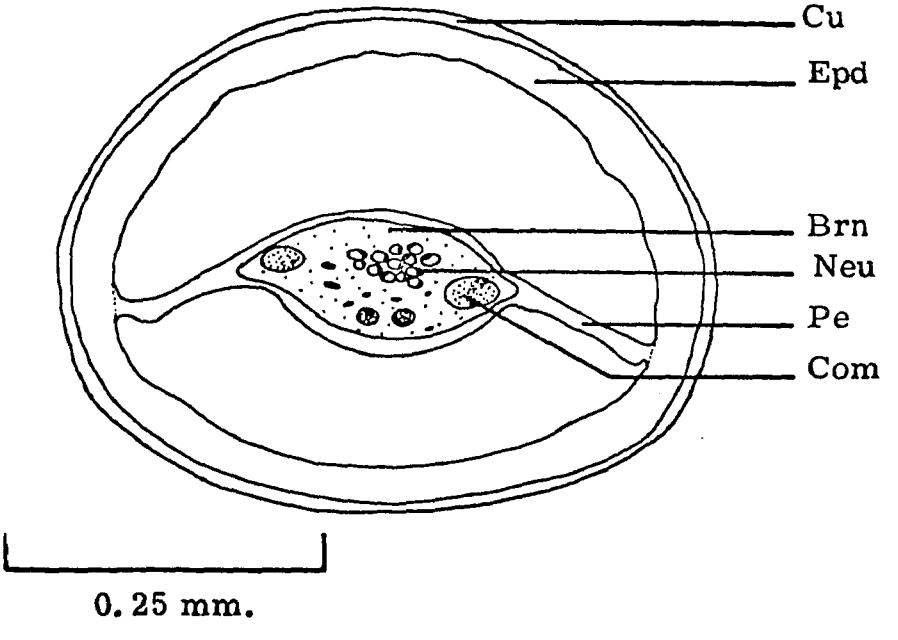


Figure 73

Figure 74. Cross section through posterior part of the brain.

Figure 75. Cross section through middle of brain.

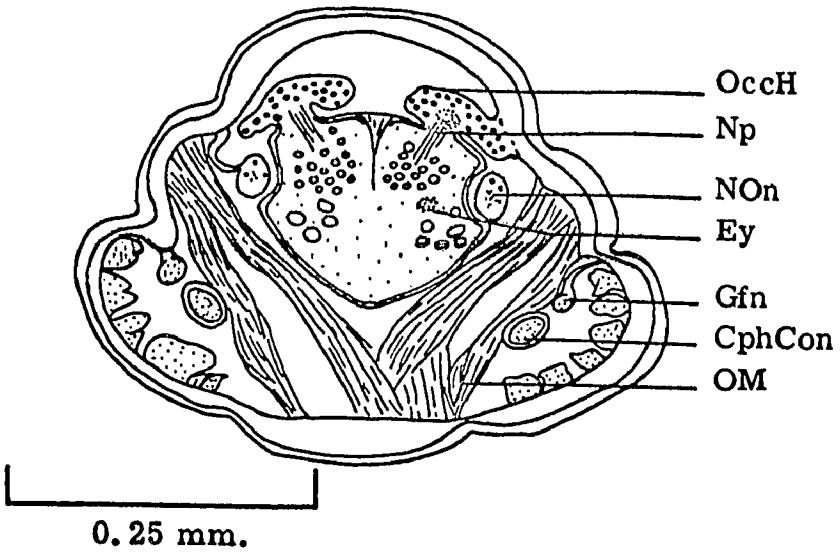


Figure 74

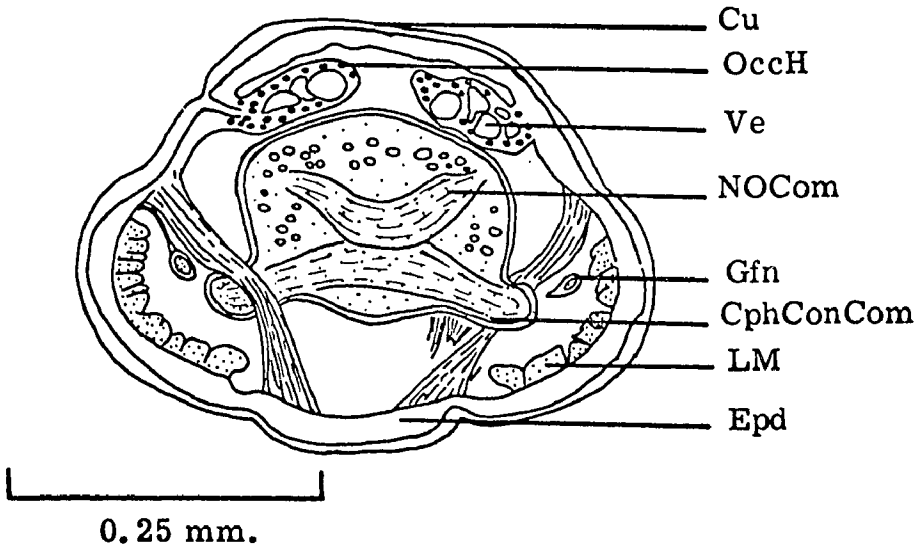


Figure 75

Figure 76. Cross section of preoral region showing nuchal organs and nuchal organ retractor muscles.

Figure 77. Cross section of the preoral region showing the musculature and the anterior ventral blood vessels near their point of origin.

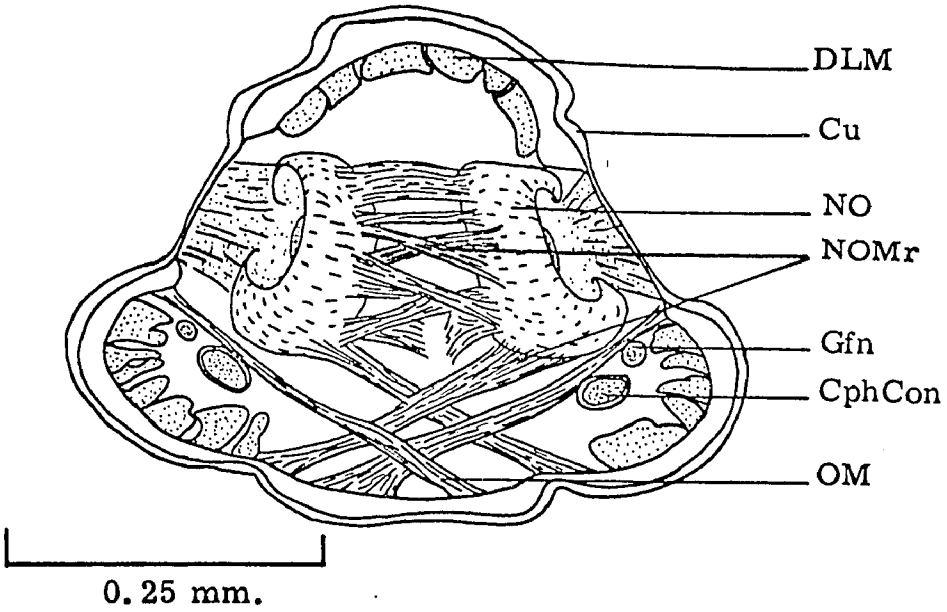


Figure 76

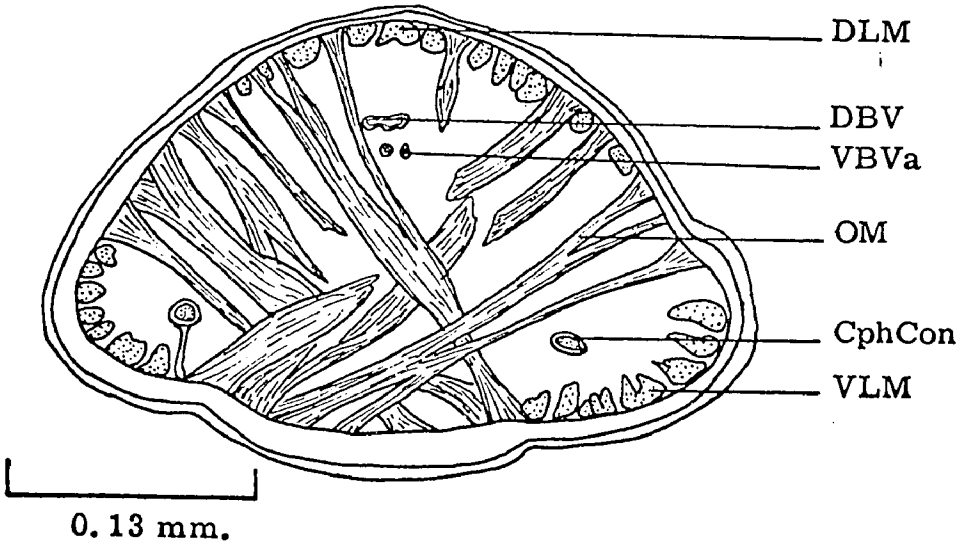


Figure 77

Figure 78. Tangential section of brain showing the fiber tract which connects the occipital horns to the central neuropile of the brain.

Figure 79. Midsagittal section of the brain.

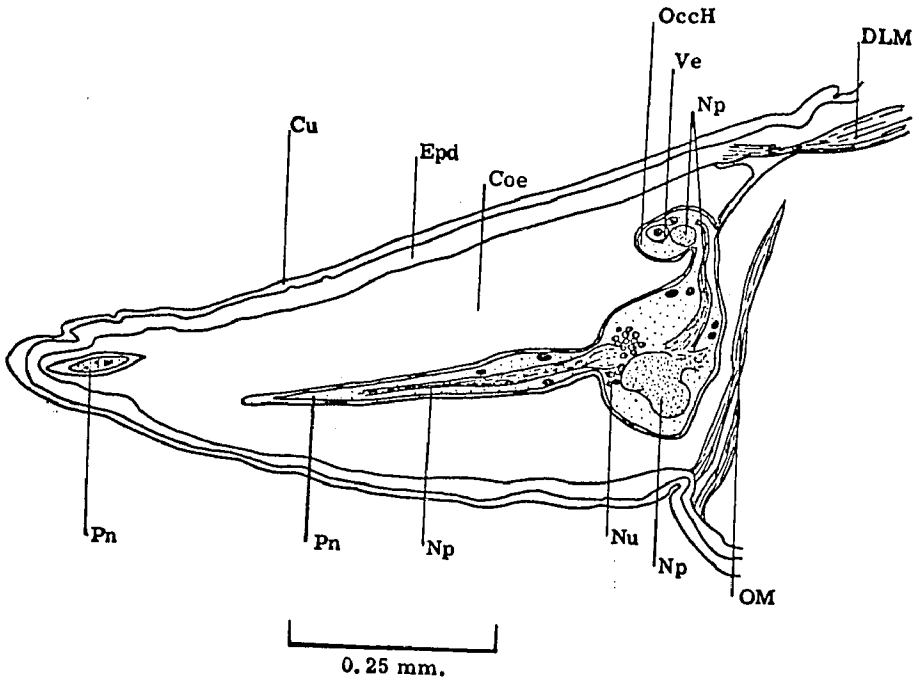


Figure 78

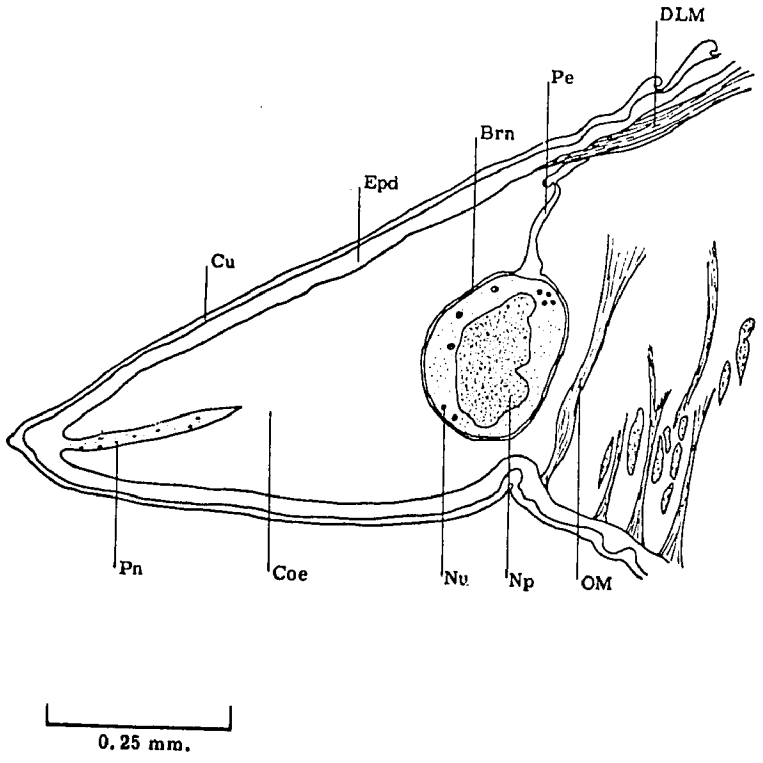


Figure 79

Figure 80. Chart of Hampton Harbor, New Hampshire. The population of Ophelia denticulata is located 250 yards west of the Hampton River bridge (near the red and black can buoy).

1206

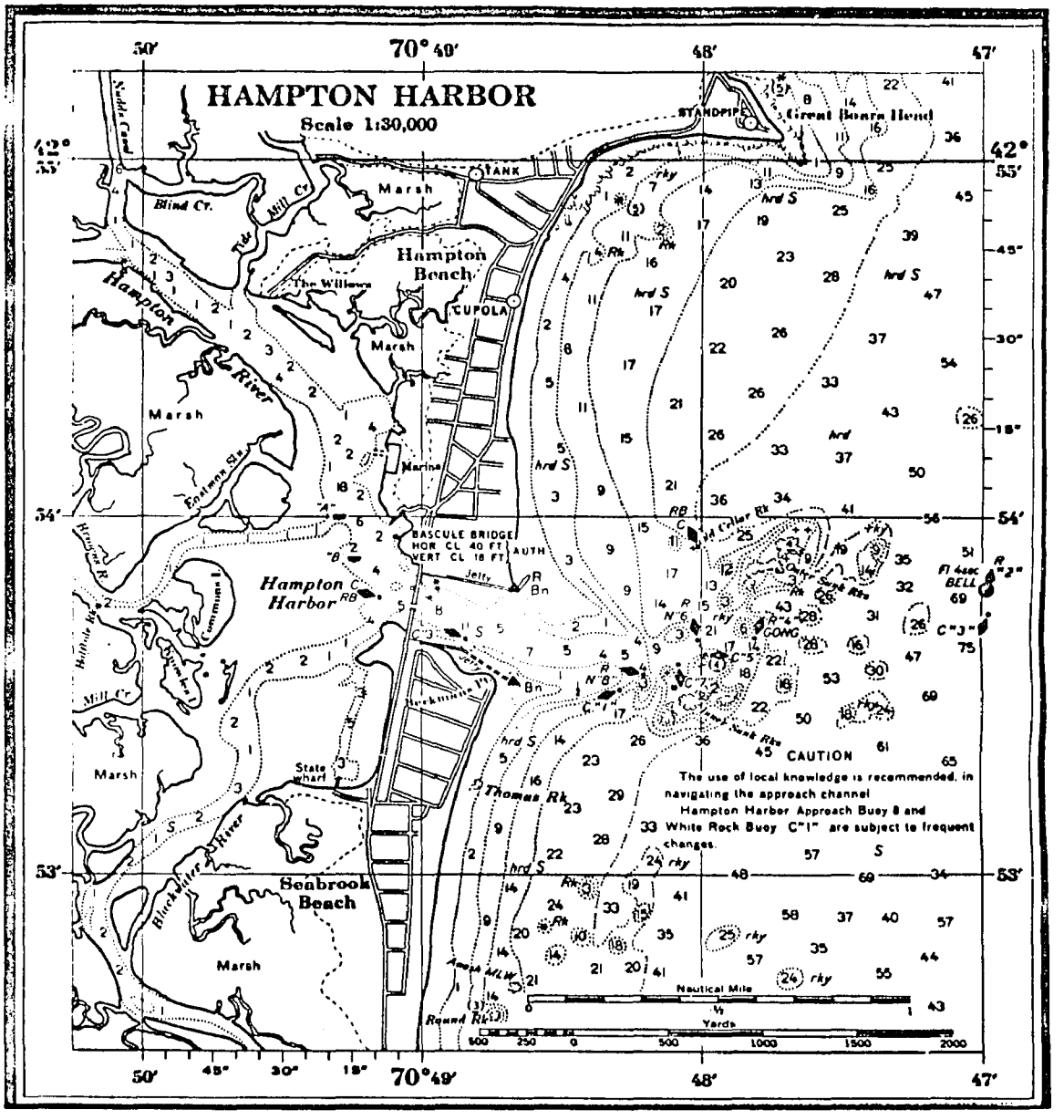
HAMPTON HARBOR
Scale 1:30,000
70° 49'
50'
48'
47'
42° 55'
54'
53'
Great Boars Head
STANDPIPE
TANK
Marsh
Blind Cr.
Tide Mill Cr.
Hampton Beach
The Willows
CUPOLA
Hampton River
Marina
Eastman Sta.
BASCULE BRIDGE
HOR CL 40 FT
VERT CL 18 FT AUTH
Hampton Harbor
Jetty
Mill Cr.
State Wharf
Thomas Rk.
CAUTION
The use of local knowledge is recommended, in navigating the approach channel
Hampton Harbor Approach Buoy 8 and
White Rock Buoy C"1" are subject to frequent changes.
Seabrook Beach
Blackwater River
Round Rk.
Nautical Mile
Yards

Fig. 80

Figure 81. Photograph of the sand bar in which the population of Ophelia denticulata is located. Copied from aerial photo 1244-25-267 taken by Aeroservice Corporation, 210 East Courtland Street Philadelphia, Penna.
Photographed November 7, 1962.
Scale approximately 1' = 570'.
Collecting site indicated by X____X.